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## THE BIOSYSTEMATICS AND EVOLUTION OF THE POLYALTHIA HYPOLEUCA COMPLEX (ANNONACEAE) OF MALESIA, I. SYSTEMATIC TREATMENT

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A component of tropical lowland rain-forest flora diversity is the presence of series of sympatric, closely related species. The three major hypotheses forwarded to explain the coexistence of such species are discussed, and an argument is presented that small, monophyletic groups are the most appropriate objects of investigation when examining them. To that end, a classification of the *Polyalthia hypoleuca* complex (Annonaceae) is provided to form the foundation for a set of forthcoming articles exploring which of the three hypotheses best applies to the complex. After presentation of evidence that the complex is monophyletic, the results of uni-, bi-, and multivariate statistical analyses of character data taken from herbarium specimens are reviewed and shown to support the delimitation of six species in the complex, with members distributed sympatrically in various combinations throughout Malesia. One new species, *P. ovalifolia*, is described. The hypothesis of coexistence that best applies to the complex is briefly noted, with supporting details to be given in subsequent articles.

*If the traveller notices a particular species and wishes to find more like it, he may often turn his eyes in vain in every direction. Trees of varied forms, dimensions, and colours are around him, but he rarely sees any one of them repeated. Time after time he goes toward a tree which looks like the one he seeks, but a closer examination proves it to be distinct.*

Alfred Russel Wallace (1878, p. 65)

*As the species of the same genus have usually, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle*

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*will generally be more severe between them, if they come into competition with each other, than between species of distinct genera. . . . One species of charlock has been known to supplant another species, and so in other cases. We can dimly see why the competition should be most severe between allied forms, which fill nearly the same place in the economy of nature. . . .*

Charles Darwin (1859, p. 76)

## INTRODUCTION

Although the prodigious organismic diversity of tropical lowland rain forests (TLRFs) is increasingly being catalogued, the biological principles generating and maintaining it remain enigmatic. This study has been conducted as part of an attempt to illuminate one aspect of the biology of tropical lowland communities that contributes to such diversity: the occurrence of series of morphologically very similar yet consistently distinct entities, or species, in apparent sympatry. In this Introduction, I first review the relevant observations and explanatory theories of previous researchers who have contemplated such series of species. Then I summarize them as a set of competing hypotheses. Finally, I outline the research methods I have used to test these hypotheses with one such series of entities. As will be demonstrated, a clear understanding of the systematics of these species complexes is extremely important to the examination of the competing hypotheses forwarded to explain their existence. I therefore include a systematic treatment of a complex of Malesian TLRF trees, the species of the *Polyalthia hypoleuca* complex (Annonaceae), that will serve as the foundation for a series of forthcoming articles investigating the outlined hypotheses with regard to this species constellation. Each of these articles will be related to and will reflect upon the data and conclusions presented in all of the others. For example, the results to be reported in subsequent papers on the distributional ecology (Rogstad, in prep. a) and floral biology (Rogstad, in prep. b) of the species included in the complex both are based on and support the systematic conclusions reached primarily on morphological grounds here.

### THE PROBLEM OF SERIES OF CLOSELY RELATED, SYMPATRIC SPECIES

One often-noted component of the high species diversity of TLRFs is the presence of series of morphologically very similar, sympatric entities (e.g., see Klopfer & MacArthur, 1961; Fedorov, 1966; Ashton, 1969; Richards, 1969; Van Steenis, 1969; Hubbell, 1979; Leigh, 1982; Whitmore, 1984). These entities are usually recognized at the species level, and because of their morphological similarity, they are presumed to be closely related species. I will give a more precise definition of these species complexes below.

That these series pose a problem for community theory can be traced back at least to the work of Lotka, Volterra, and Gause (Hardin, 1960; Armstrong & McGehee, 1980). Gause demonstrated experimentally that the predictions of the Lotka-Volterra equations were fulfilled in competition experiments between two closely related *Paramecium* species. This principle is usually referred



to as Gause's Principle of Competitive Exclusion: two or more species that occupy the same niche cannot coexist in the same habitat.

While theoreticians (e.g., Hubbell, 1979; Huston, 1979; Armstrong & McGehee, 1980; Pickett, 1980; Agren & Fagerstrom, 1983) have argued that this principle probably is not valid for nonequilibrium environments, a large body of empirical evidence (see, for example, MacArthur, 1957; Hutchinson, 1959; Mayr, 1963, 1970; Schoener, 1974, 1983; Harper, 1977; Jones, 1978; Werner, 1979; Aarssen, 1983, 1985; Armbruster, 1985; Pulliam, 1985), based primarily on geographic distributions or niche shifts of closely related species, suggests that it generally holds, at least in temperate environments. The many studies on character displacement (e.g., Grant, 1972) are also germane, because they indicate that even species without broad overlap in many niche characteristics may compete intensively with regard to the overlapping areas.

For temperate trees, the prevailing belief has been summed up by Fedorov (1966, p. 1): "... taxonomically close ... species of plants, do not as a rule occupy the same area, but are most usually geographically isolated from one another ... the isolation of closely allied species may be not only geographical, but ecological as well, as when such species are found in different habitats within one area." According to V. Grant (1963), this principle becomes more evident as the size of the organisms under consideration increases, due to more intense competition for scarce resources among larger organisms. He cited several temperate examples of this concept, noting that while some herbs may have series of sympatric, closely related species, this condition is rare for trees. Two often-noted, seeming exceptions (members of the genera *Quercus* and *Pinus*) show, upon detailed examination, clear geographic or ecological separation of closely related species (also see Stebbins, 1950; Reich & Hinckley, 1980). There may be a few groups of temperate trees that do not conform to Gause's Exclusion Principle, but these should generally be regarded as the anomalies that highlight the rule.

In contrast, forests of the humid tropics often appear to deviate significantly from Gause's principle. For example, in Ashton's (1977, 1984) surveys of five two-hectare (ha) plots in TLRF at Pasoh Forest Reserve (central peninsular Malaysia), 484 species were identified (DBH > 10 cm); approximately 40 percent of the 191 genera had three or more congeners, and 15 percent of the genera had six or more congeners. Some genera had many species, with *Eugenia* topping the list at 28. Viewed in another manner, if (as Ashton extrapolates) 700 species can be found on 50 ha at Pasoh, more than 300 (43%) will be growing sympatrically with at least five congeners. Interestingly, Pasoh is by no means the most species rich of the forests that have been surveyed in Malesia (Ashton, 1984), so even more striking examples probably exist. Sympatric ensembles of closely related species also exist in the richest TLRFs of South America, such as the Yanomamo region of Amazonian Peru, and in Africa, where *Cola* (Sterculiaceae) and *Diospyros* (Ebenaceae) are examples of genera exhibiting this pattern (A. Gentry, pers. comm.). Thus, while the intensity of this phenomenon may vary from region to region, it appears to be a general feature of TLRF communities.

As noted above, the occurrence of sympatric, closely related species is not



cause to discard the Competitive Exclusion Principle if such species are found to have diverged in at least one niche characteristic. However, it will be seen below that some authors have argued, on both theoretical and empirical grounds, that series of closely related species may coexist in forests of the humid tropics without such niche divergence. Are there fundamental differences in temperate and tropical forests in the forces guiding evolution and community organization?

#### DEFINITIONS

Greater precision can be given to the above concepts, and to the development of a means to investigate them, by defining a few of the terms more rigorously. The term "sympatry" has a long and varied history of usage (e.g., see Mayr, 1970). Here I use it to mean the concurrent, regular occurrence of different taxa within potential gene exchange distance of one another. This rather broad definition has been chosen over more restrictive ones that may overlap with niche definitions (e.g., ecological or temporal sympatry).

The concept of the niche has also been extensively debated (e.g., see discussion in Aarssen (1983)). I use Whittaker's (1967, p. 210) definition: "the position of the species in the community, its particular way of relating to other species, environment and space within the community, and seasonal and diurnal time." A niche difference between two tree species exists if they interact with other species differently (e.g., pollinators or herbivores), if they differ in some aspect of the environments and space they occupy (e.g., understory vs. canopy; differences in substrate requirements), or if their seasonal or daily rhythms of activity differ temporally (e.g., flowers functional at different times of the year or day).

It is also not always clear what is meant by the various authors cited above when they use concepts such as "morphologically very similar," "closely related," "taxonomically allied," or "congeneric." All of these expressions refer to groups of species whose members are assumed to have a close phylogenetic relationship. However, they are relative, depending upon context, and they can be (and have been) applied to different types of groups. Several discussions of the types of groups that can be constructed exist in the literature (e.g., see Wiley, 1981), but for present purposes I will follow Eldredge and Cracraft (1980) in reducing the possibilities to two main classes, monophyletic and nonmonophyletic groups. As will be seen below, these groups differ as to their precision in delimiting assemblages of species with immediate phylogenetic proximity. After a brief explanation of the differences in the construction of these two types of groups, the importance of the type chosen to examine the phenomenon of series of "closely related" sympatric species will be outlined. I will establish that monophyletic groups are preferred over nonmonophyletic ones in investigating this phenomenon.

A comparison of these two types of groups is presented in FIGURE 1. In this discussion, it is assumed that the phylogenetic relationships among the taxa (designated by letters) as drawn reflect the "true" history of the groups.

Monophyletic groups, as defined by Hennig (1966), comprise all and only



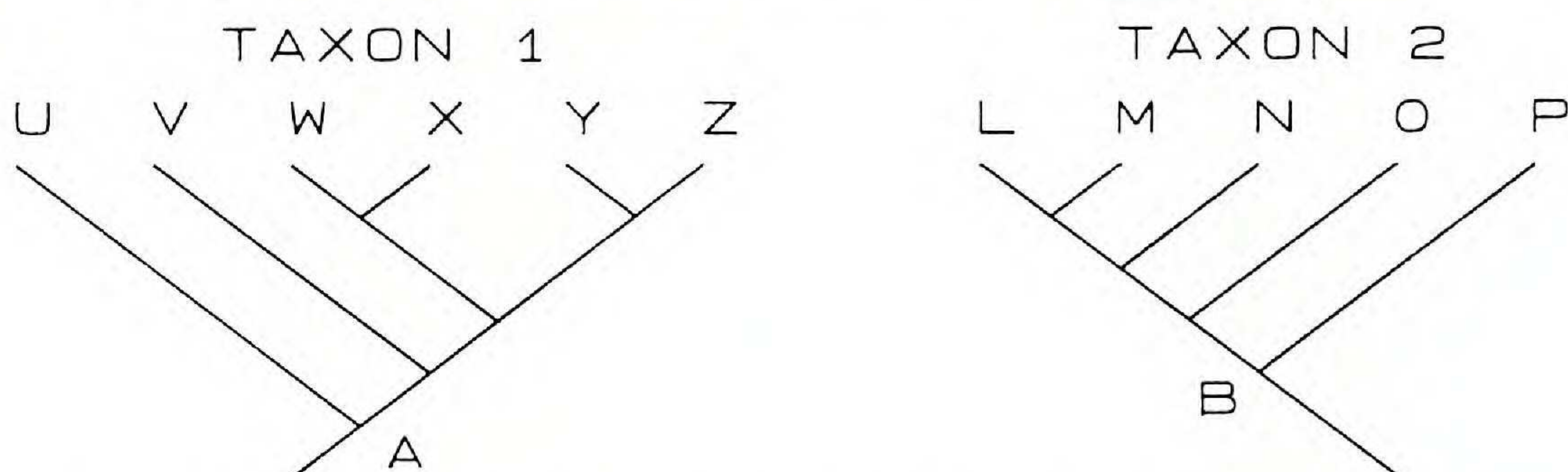


FIGURE 1. Monophyletic and nonmonophyletic groups (see text for explanation).

those taxa descended from a common ancestor (the “strict” monophyletic groups of Stevens (1986)). Examples include such terminal groups as W and X (note that these are sister taxa); W, X, Y, and Z; or all of taxon 1, in which case node A may be considered as the common ancestor. Monophyletic groups are usually recognized by the presence of a unique character or suite of characters (synapomorphies) that is shared among all the members of the group and that presumably arose only once in the ancestral lineage before its diversification. Nonmonophyletic groups do not include all and only the species descended from a single ancestor but rather exclude at least one of the terminal taxa. For example, nonmonophyletic groups would include, for taxon 1, ones made up of only V, W, and Y, or of V, W, X, and Z (often referred to as “paraphyletic” groups). They can also be constructed of taxa with even more distant phylogenetic relationships such as only taxa V, Y, and M (they are then frequently termed “polyphyletic”). While monophyletic assemblages are by definition composed of taxa with the most immediate phylogenetic relationships (the *most* closely related contemporary species), nonmonophyletic groups exclude some of these taxa.

#### THE NEED FOR MONOPHYLETIC GROUPS

Of these two types of groups, small monophyletic ones will always be most informative in examining whether or not series of “closely related” species live in sympatry in TLRFs. Although series of apparently sympatric, congeneric species have been identified at several tropical forest sites (e.g., see Ashton, 1977; Wheelwright, 1985), a phylogenetic perspective of these genera is required to demonstrate that any particular congeners occurring at one site can be considered to be members of a small monophyletic group. For example, the genus under investigation here, *Polyalthia* Blume, comprises up to 150 species, nine of which have been found at Pasoh Forest Reserve, Peninsular Malaysia (P. S. Ashton, pers. comm.). If, upon analysis of the systematics of the entire genus, no two of these nine species can be placed together in a small monophyletic group, and all nine are best described as phylogenetically distant from one another within the genus, then making a case that a series of “closely related,” sympatric species of *Polyalthia* occurs at Pasoh becomes more difficult. In studying this interesting ecological phenomenon, then, a clear understanding of the systematics and biogeography of the group is crucial.



If, as is widely believed (e.g., see Mayr, 1970) allopatric speciation is more prevalent than other modes of speciation, it might be expected that sister species, especially recently derived ones, will rarely occur in sympatry. The term "monophyly" has nothing to do with age, of course, yet when most or only some of the members of a small monophyletic group are found sympatrically, their coexistence is still of interest as they are perhaps the most closely related entities of the group that can be found growing together in nature.

For several reasons, either small monophyletic groups or those including only all the species of a small monophyletic group that occur in sympatry locally are also preferred over nonmonophyletic groups when investigating the origin and maintenance of series of "closely related" sympatric species with regard to competitive exclusion. First, if nonmonophyletic groups are chosen to examine "closely related" species in sympatry, it is possible to miss one or more interactions between sympatric species of closer phylogenetic relationship than those studied. As an example, consider a forest where all of the congeneric species of taxon 1 in FIGURE 1 are known to occur in sympatry. If an investigator chooses to study only species V and X and finds that they have differentiated niches, the implications of this finding would have to be revised if, later, no niche differences could be detected among species V, W, Y, and Z. Alternatively, an investigator might find an extensive and seemingly random pattern of overlap with regard to some niche gradient measured for all of the species of FIGURE 1 but may discover well-differentiated patterns when comparing only the members within taxon 1 or taxon 2.

Another approach to understanding why small monophyletic groups are preferred in addressing the problem of series of closely related, sympatric species derives from a consideration of how phylogenetic distance may be related to niche distance. It is thought often to be the case that, *ceteris paribus*, the closer the degree of phylogenetic relationship, the greater the degree of morphological similarity. It follows that monophyletic groups are often (although not always) those with the greatest degree of morphological similarity among member taxa. If structure is related to function, then members of monophyletic groups should have the most similar niches. It is also often argued (e.g., see Grant, 1963; Wheelwright, 1985; Glazier, 1987) that since most closely related species have the same ecological and physiological heritage via their common ancestral lineage, such species will usually have relatively similar niches (for a contrasting view, see the discussion of the adaptive speciation model, below). This principle has been invoked, at least implicitly, in many of the experimental studies purporting to investigate competitive exclusion, beginning with Gause's experiments with two *Paramecium* species. Studying the niche characteristics of the members of monophyletic groups ensures that the most closely related entities at a site are under consideration and therefore provides the most rigorous test of whether or not sympatric closely related species show niche differentiation.

Finally, if one is interested not only in present patterns (for example, patterns of niche differences of contemporary species) but also in evolutionary processes, monophyletic groups are again the more informative type. To use another illustration from FIGURE 1, if sympatric species U and Z are found to have



only slight niche differences, this might be interpreted as indicating a minimal degree of niche divergence from the state of their common ancestor at node A. However, if niche characteristics of V, W, X, and Y are subsequently found to diverge greatly in a similar fashion from U, then it is most parsimonious to interpret the slight differences between U and Z as convergence.

In conclusion, monophyletic groups are the preferred groups for interpreting the biological significance of series of sympatric, closely related species. Such groups are composed of the most phylogenetically recent products of speciation, and thus their members are always the most closely related species that can be investigated when considering any lineage. Only the study of monophyletic groups gives a minimal estimate of the total extent of niche divergence of a lineage radiating from a common ancestor and may yield information about this divergence in relation to speciation and the total pattern of the geographic distribution of the descendant species. As speciation is the wellspring of diversity, an understanding of sympatry-allopatry patterns in relation to niche divergence within small monophyletic groups will be informative as to the origin and maintenance of TLRF diversity.

Unfortunately, most, if not all, of the studies purporting to investigate sympatric, closely related species were carried out at a time when such considerations concerning monophyletic groups were not appreciated. For example, several studies have examined flowering phenology and have arrived at a range of conclusions for different groups. However, what appear to be either random or highly organized patterns of flowering may require reinterpretation in relation to new information concerning the monophyly, phylogeny, and biogeography of the taxa involved (or a more inclusive set of taxa), if monophyletic groups have not been used in such studies. With this caveat in mind, it is important to note that, as will be shown in the systematic treatment below, congeneric groups are by no means necessarily monophyletic ones.

#### PREVIOUS OBSERVATIONS AND HYPOTHESES

##### **Hypothesis I. Polymorphic Entities**

One explanation of monophyletic series of sympatric species in TLRFs is that the phenomenon has been largely misinterpreted: many or all of the members of such series are more appropriately combined into single polymorphic species (e.g., see Levin, 1979). To establish, on morphological grounds, that this is the case for any group of entities, at least one of three fundamental patterns of morphological variation must be demonstrated for the group. The first consists of a few or many characters that are extremely variable on a local scale. The second has been termed "kaleidoscopic" character distributions (Cullen, 1968). In this case, the possible character states for a number of characters exhibit several or all of the possible permutations among taxa. While Cullen used this term to indicate patterns of characters among species, it is also applicable at other levels. The third pattern, clinal variation (e.g., see Mayr, 1970), can lead to problems of classification when two taxa from distant sites are recognized as distinct until morphologically intermediate specimens are found. However, even if local species can be thus "explained away," local



differentiation may be biologically significant despite a broader geographic pattern of kaleidoscopic or clinal variation within a taxon. Hence, Leenhouts's (1967) reduction of approximately 255 species of *Allophylus* (Sapindaceae) to one, Jacobs's (1962) similar reduction of species in *Pometia* (Sapindaceae), and descriptions of variable taxa such as *Diospyros* (Ebenaceae) species by White (1962), *Ficus deltoidea* Jack (Moraceae) by Corner (1970), *Drimys piperita* Hooker f. (Winteraceae) by Vink (1970), *Licania* (Chrysobalanaceae) species by Prance (1972), *Calophyllum blancoi* Planchon & Triana and *C. canum* Hooker f. (Guttiferae) by Stevens (1980), *Calamus* (Palmae) species by Dransfield (1981), and *Chisocheton* (Meliaceae) species by Mabberley (1979), among others (see list in Leenhouts, 1967), are difficult to interpret. Some may indeed be examples of taxa in which a high degree of polymorphism leads to problems of definition of morphological species.

In this context species delimitations based upon morphological criteria may require revision as new data from allied studies (e.g., chemosystematics, reproductive biology, or ecology) accumulate, since such new information may not support the decisions based upon morphological patterns alone (Raven, 1976; Levin, 1979; Stevens, 1980). Collections for the great majority of tropical taxa are sparse, and as areas become more thoroughly studied, any one of the above possibilities might alter taxonomic decisions about groups previously recognized as species rich.

It is important to note here that hybridization and hence hybrid swarms are thought to be rare in TLRFs (Ashton, 1969, 1984; Burger, 1980). On the other hand, if it is determined that facultative apomixis occurs to a significant degree in TLRF communities (Kaur *et al.*, 1977; Jong, 1980; Kaur, 1980), then polymorphic apomictic assemblages are to be expected (V. Grant, 1971). A high degree of polymorphism may also be expected for species in which inbreeding is the rule. On theoretical grounds the latter has been proposed as the case for trees of the humid tropics (Corner, 1954; Baker, 1959; Fedorov, 1966; Van Steenis, 1969; but see Chapter 4 in Rogstad, 1986).

## **Hypothesis II. Groups of Discrete, Closely Related Species Do Occur in Sympatry**

Various investigators (references below) have accepted that a number of these complexes comprise discrete, sympatric species, and two further hypotheses have been forwarded to explain their existence.

**HYPOTHESIS IIA. SPECIES HAVE OVERLAPPING NICHES.** It has been suggested that members of such series may have similar or identical niche characteristics; sympatry here contradicts the competitive exclusion principle, or at least the observations on temperate forest communities noted above. This line of thought has developed from empirical observations, as well as from theoretical considerations of evolutionary and community-organizing forces occurring in TLRF communities. Fedorov (1966, 1976), Poore (1968), Richards (1969), Van Steenis (1969, 1976, 1981), Baker (1970), Wong and Whitmore (1970), Hubbell (1979), Ashton (1979, 1984), Gan *et al.* (1981), Tanner (1982), Yap (1982), and Wheelwright (1985) have all discussed examples where no evidence could



be found of niche divergence or niche specialization among sympatric groups of TLRF tree species (also see Klopfer & MacArthur (1961) and Terborgh (1985a) for interesting studies of TLRF birds).

It has been proposed that in many cases where series of very similar species are sympatric in TLRFs, the distinguishing morphological characters are not associated with differences in niche parameters, implying that these series arise not by differential adaptation but rather by selection-neutral processes. Noting that correlates of the high species diversity of these forests are a low density of individuals and, therefore, a small effective population size for most species, Fedorov (1966) suggested that these conditions favor speciation by random drift. His proposal stems, in part, from the work of Wright (1931), who presented a population genetics model in which random fixation of changes in gene frequencies (drift) is likely in organisms with small effective population sizes. If gene flow among small populations is consistently low, speciation by random drift results (King & Jukes, 1969; Maynard Smith, 1970; Stern & Roche, 1974; Bernstein *et al.*, 1985; Slatkin, 1985).

Hubbell (1979) and Ng (1983) have demonstrated that a large percentage of the species found locally in TLRFs exhibit extremely low population numbers and patchy distributions. For example, Ng examined Poore's (1968) data and determined that of the 377 species identified on 23 ha of peninsular Malaysian TLRF, 307 (81%) had ten or fewer mature individuals and 143 (38%) were represented by only one (see Lovejoy (1975) and Terborgh (1985a) for parallel results with TLRF bird species). Such low population densities and patchy distributions of species increase the chances for disruption of gene flow by population isolation, leading to heightened localized inbreeding, and therefore also increase the chances for random drift. For an even more radical yet supportive view, see Barton and Charlesworth (1984).

In this connection, several authors have indicated that since tropical forests are less seasonal than temperate ones, the environmental cues triggering intraspecifically synchronized flowering in temperate forests are largely absent. Flowering within local populations of some species of TLRFs may thus be asynchronous (Holttum, 1953; Koriba, 1958; Fedorov, 1966; Wong, 1983). The occurrence of noncoordinated flowering within species with small population sizes would act to inhibit gene exchange even further and would promote random drift.

The few investigations documenting levels of gene flow for TLRF tree populations (Whiffin, 1978; Chan, 1980; Gan *et al.*, 1981) give evidence that gene exchange is very local and occurs at low levels. In addition, Lovejoy (1975) and Terborgh (1985a) have shown that a large proportion of the birds found in TLRFs have low population densities and very low vagility. Similar patterns have been found for TLRF canopy insect species (Elton, 1975). Gene dispersal in TLRF tree populations will be commensurate with the density and the degree of vagility of their pollen and seed vectors.

Lewis's (1966) suggestion that small populations with a high degree of inbreeding are more susceptible to novel chromosome rearrangements that potentially lead to speciation is worthy of consideration with respect to TLRF tree population structure (also see Bush, 1981). It is important to note that



speciation via such changes no longer necessarily requires the troublesome bottleneck of Goldschmidt's (1940) hopeful monsters but rather may occur through genetic phenomena in small populations (Dover & Flavell, 1982; Rose & Doolittle, 1983; Fitch & Atchley, 1985; Wallace, 1985; Kriebler & Rose, 1986).

Several authors (e.g., Fischer, 1960; Baker, 1970; Stebbins, 1974; Van Steenis, 1978) have argued that tropical environments are more stable than temperate biomes with respect to the degree and predictability of the fluctuations of physical parameters and are therefore more neutral in selection of variation by physical extremes. In other words, TLRFs are benign environments where a greater degree of marginal or nonselected variation persists. Many of the characters distinguishing among similar species are apparently not adaptive (e.g., see Ashton, 1979) but have arisen through genetic discontinuities originating in stochastic processes (drift) and are functionally of little consequence (Van Steenis, 1969, 1976, 1978). A contrasting view of the effects of relaxed abiotic selection in TLRFs is presented below.

Another theoretical approach that predicts little chance for niche differentiation within complexes of similar species (or among anything but very general guilds of species, for that matter) derives from community-level considerations. If TLRF communities are nonequilibrium communities (Connell, 1978; Hubbell, 1979; Acevedo, 1980, 1981; Chesson & Warner, 1981; Abugov, 1982; Wright & Hubbell, 1983) the composition of any local biota may be more a product of historical chance events than of the relative competitive interactions of the species involved. The taxonomic assemblage at any locale is constantly and randomly changing, a phenomenon that Hubbell (1979) has termed "community drift." Several authors (e.g., Aubréville, 1938, 1971; Grubb, 1977; Strong, 1977; Ewel, 1980; Lang & Knight, 1983; Brokaw, 1985; Lieberman *et al.*, 1985) have noted the importance to all TLRF tree species of regeneration at tree-fall sites. If successful reproduction is largely dependent on having progeny in the appropriate stage of development present in unpredictable forest gaps, then forest structure has a proportionately large stochastic component (Connell, 1978; Burger, 1980; Buckley, 1983; Connell *et al.*, 1984; Comins & Noble, 1985). Since most TLRF species have extremely low population densities, if the community-drift hypothesis holds most TLRF species will be randomly associated through time. Competitive interactions between or among species, as well as resource availability, will be completely unpredictable, and therefore persistent directional selection will be rare. Such stochastic competition and distribution of resources may lead to selection for generalists (Went, 1973; Hubbell, 1979; Burger, 1980; Buckley, 1983; Ashton, 1984) and thus act upon a significant portion of TLRF species by generalizing their niches rather than driving niche divergence.

The consequences of nondirectional selection can also be explored in more formal terms. Kimura and Weiss (1964) and Kimura and Ohta (1971) have shown that in diploid populations, mutations become fixed predominantly by random drift when the quantity  $4N_e s$  ( $N_e$  represents the effective population size, and  $s$  denotes the coefficient of selection) is sufficiently smaller than 1 (for example, Hartl and colleagues (1985) suggest when  $4N_e s < 0.1$ ). In tropical



humid forests the unpredictability of both one's competitors and the matrix of available resources over long periods of time may give vastly varying and often conflicting values of  $s$  for most alleles, thus reducing the value of  $s$  to close to 0 (selection nondirectional). As  $s$  approaches 0,  $4N_e s$  becomes  $\ll 0.1$ , and this is exacerbated by the small population sizes found in TLRF trees. Lande (1976) has presented a model that suggests phenotypic evolution may be subject to drift even in large effective populations where selection is weak. A few empirical studies (Malecot, 1959; Selander, 1970; Carson *et al.*, 1982) have shown that when directional selection is weak or nonexistent, character variability may increase or drift.

The link between the theories of community drift and the random drift of species in TLRF communities (and the implications of this link for niche divergence of sister species descendent from a TLRF tree ancestor) is perhaps best established by considering the most widely accepted model of speciation, an allopatric one. Under this model, two lineages from a common ancestor first become geographically isolated. Due to the low population sizes common to TLRF trees, random sampling of the once-common genetic pool and accumulation of different mutations in the two isolated lineages lead to genetic divergence of the daughter populations. Gottlieb (1984, 1985) has pointed out that many of the morphological differences distinguishing species are under simple genetic control involving a low number of alleles, a situation facilitating rapid fixation of morphological differences by random drift. Since competitors and resource distribution are unpredictable, no directional selection takes place. Divergence is due to genetic sampling errors only, and morphological differences need not have any pronounced functional significance (Van Steenis, 1978, 1981; King, 1984; Davis & Gilmartin, 1985), especially if selection for generalists prevails. If the two sister lineages subsequently achieve sympatry, it is highly unlikely, due to the extremely low population numbers and densities of species in TLRF tree communities, that the two lineages will ever compete over resources in any predictable manner; therefore, the forces driving competitive exclusion and niche divergence (or character displacement) envisioned as active in temperate communities will be extremely weak in TLRF communities. Daughter populations that have diverged morphologically and genetically (to a degree that they have become genetically incompatible) may coexist indefinitely in TLRF communities without having diverged with regard to realized niche characteristics. Community drift and random drift thus may interact to generate series of closely related, sympatric species with broad niche overlap in these biomes.

**HYPOTHESIS IIB. SPECIES HAVE DIVERGENT NICHES.** An alternative hypothesis has also been forwarded to describe the sympatric occurrence of series of closely related entities (e.g., species), granted that it can be demonstrated that distinct entities exist. A number of authors have argued that similar species coexist in TLRFs by occupying narrowly defined, distinct niches, thereby not engaging in competition along at least one niche gradient. Wallace (1878, p. 66) noted that, "In the equatorial zone, there is no struggle against climate." The forces of natural selection arise from biological interactions rather than physical con-



straints, leading “. . . to the filling up of every place in nature with some specially adapted forms.” Dobzhansky (1950) and Williams (1964) have reemphasized that biological competition is the most important factor in natural selection in the tropics (as opposed to physical environmental factors in temperate forests), and that this has led to more specialization for narrow niches and, in turn, a greater diversity of species.

Dobzhansky (1950) also pointed out that TLRFs have a greater variety of niches than other terrestrial forest habitats due to their greater structural complexity, a notion that has been further reinforced by Corner (1954), Ricklefs (1977), and Terborgh (1985b). If this is true, the higher structural heterogeneity of TLRF communities would increase the possibilities for the coexistence of similar, closely related species, each with a distinct niche, thereby permitting greater species packing.

Ashton (1969) has proposed that such series of species may be the result of adaptive speciation (see Ringo *et al.*, 1985, for a summary of the model). Each species in such a series may actually have subtly different niche characteristics with respect to at least one resource gradient. Such niche differentiation may take place with allopatric speciation or occur through divergent selection driven by competition between sister species once they come into sympatry again.

Studies of TLRF organisms reporting empirical evidence of similar, closely related species each having at least one unique niche characteristic and growing sympatrically include those by Snow (1965), Diamond (1973), Burger (1974, 1980, 1981), Vandermeer and colleagues (1974), Stiles (1975), Gentry (1976, 1982), Chan and Appanah (1980), Janzen (1980), Haber and Frankie (1982), Fleming (1985; although significant overlap was found for all parameters examined), Martin (1985), and Moulton (1985).

Burger (1974, 1981), Stevens (1980), and Ashton (1984) have argued that in many cases, sister species grow allopatrically in the tropics. Such patterns, however, need careful scrutiny, as they may reflect more about how taxonomists recognize taxa than about anything of biological significance (Stevens, 1980) and may therefore falsely support Gause's conclusions.

#### A METHOD OF EXAMINING THE COMPETING CONCEPTS

Most of the theorizing and supporting evidence reviewed in the paragraphs above are based on preliminary, descriptive, or anecdotal information. The monophyly of the groups discussed has not been established, and quantitative studies of character-state variation within and among putative entities to establish their delimitation are lacking. Further, attempts to demonstrate the sympatry of distinct entities of advocated monophyletic groups, and then to distinguish whether the entities of such a complex are in fact ecologically equivalent or rather have differentiated with respect to one or more niche characteristics, have been neglected.

Obviously, a clear understanding of the taxonomy of the members of any group intended for such investigations is crucial. Attempting to compare niche characteristics of sympatric entities whose definitions as species are not well understood will most likely be misleading. The following systematic treatment



of the *Polyalthia hypoleuca* complex is the foundation for a series of articles in which I will address all of the concerns noted in the previous paragraph, thereby enabling a choice of which of the above three hypotheses is most applicable with regard to this group of taxonomically allied Malesian tree species.

To examine whether or not the niches of the species in this complex were segregated in any way, I employed methods commonly used to define niche characteristics for temperate plants, recognizing from the outset that this approach might yield only negative evidence. That is, the failure of these methods to detect niche differentiation would not eliminate the possibility that niche differentiation does exist between entities for one or more uninvestigated features. Nevertheless, the finding that two morphologically similar species have similar or identical niche characteristics as defined by techniques that have successfully detected niche differentiation in temperate plants is theoretically interesting and prepares the ground for alternative or more detailed future investigations. However, as will be seen in the subsequent associated articles, such negative evidence was not a problem in this case. In fact, information concerning the niche characteristics of the species of this complex serves to support my systematic conclusions and must thus be consulted if one is interested in understanding the sum of the evidence speaking to the systematic decisions, based primarily on morphometric analyses, presented here.

Only one group was examined in this research. A number of them will have to be investigated with regard to these hypotheses before we can do much more than speculate about the causal forces generating the patterns. Information on these issues is central to understanding the origin and maintenance of TLRF diversity. A forest structured predominantly under hypothesis I is a very different community than one composed of groups conforming strictly to hypothesis IIB. Of course, a range of possible combinations between these two extremes is probable locally (will generalizations be possible at more synoptic levels?), and a more accurate description of the distribution curve for the realized possibilities will yield deeper insight into evolutionary processes in TLRF biomes, as well as have implications for forest utilization and management practices.

#### SYSTEMATICS OF THE POLYALTHIA HYPOLEUCA SPECIES COMPLEX

After examining several groups of potential candidates for this investigation, I chose the *Polyalthia hypoleuca* complex. I was able to determine several characters suggesting that it was a monophyletic group, and in preliminary field work I found that some of the species do grow in sympatry in statistically tractable sample sizes.

The specific goals of this systematic treatment are to demonstrate that this complex of species is indeed monophyletic, to apply various morphometric techniques to support the conclusion that discrete entities (morphological species) exist within this monophyletic group, and to present a formal classification for the group.



THE GENUS *POLYALTHIA* AND THE PLACEMENT OF THE  
*P. HYPOLEUCA* COMPLEX

*Polyalthia* comprises approximately 100 to 150 species and is therefore one of the larger genera of the Annonaceae. Members of the genus are generally restricted to tropical latitudes and lower altitudes. They are distributed in humid regions of Africa and Madagascar, and from India and Sri Lanka through Southeast Asia and Malesia to Fiji and the associated islands. Sinclair (1955), the last author to revise a significant portion of the genus, placed it in tribe Unoneae, which he defined primarily on the basis of a single character: petals that are valvate in the flower buds. This agrees with the placement of the genus by other systematists, including Bentham and Hooker (1862), Fries (1959; he further subdivided the tribe into informal groups, *Polyalthia* being placed in the *Polyalthia* group), and Hutchinson (1964; *Polyalthia* is placed in Group A of subtribe Xylopineae). In contrast, Walker (1971) included *Polyalthia* in his tribe Uvarieae, based upon considerations of pollen morphology.

However, all of these classification schemes need further investigation. For example, as is shown in FIGURE 2, within the *Polyalthia hypoleuca* complex, which as I shall demonstrate below is clearly monophyletic, some members (e.g., *P. discolor* Diels) have petals that are distally (but not basally) imbricate in the floral buds, while at least one (*P. glauca* (Hassk.) Mueller) apparently has only valvate petals. Imbricate bud petals have been noted for other species in *Polyalthia* and in other genera usually placed in the Unoneae (Okada & Ueda, 1984; pers. obs.), suggesting that the distribution and the taxonomic importance of this character are in need of review. Further examinations of petal aestivation should include observations on degree of petal overlap, and whether the petals overlap distally, basally (including insertion), or both.

Indication that previous treatments are in need of further scrutiny also derives from Walker's (1971) observations that two species of *Polyalthia* differ in pollen characters from the other congeners examined. These characters, as well as several other nonpollen characters (discussed below), unite these two species with four not examined by Walker, and the mutual possession of these characters constitutes the evidence for the monophyly of the *P. hypoleuca* complex (the pollen data will be treated in detail in Rogstad & Le Thomas, in prep.). The pollen morphology of these species is different from that of the other *Polyalthia* species examined to date, with the few important exceptions discussed below.

It is difficult to reconcile the pollen characters of the *Polyalthia hypoleuca* complex with those of Walker's Uvarieae, to which other members of *Polyalthia* conform (see also Le Thomas, 1988). The distally imbricate floral bud petals and the distinguishing pollen type within the complex render its placement both within the genus and within the subfamilial classification proposals noted above problematic. Thus, the clearly monophyletic *P. hypoleuca* complex may be the sister group to some taxon in another tribe, or it may be derived from within *Polyalthia*. Until the phylogenetic relationships of the complex are more clearly understood, assigning new generic or sectional status to this constellation of species may create future nomenclatural problems. Thus, for



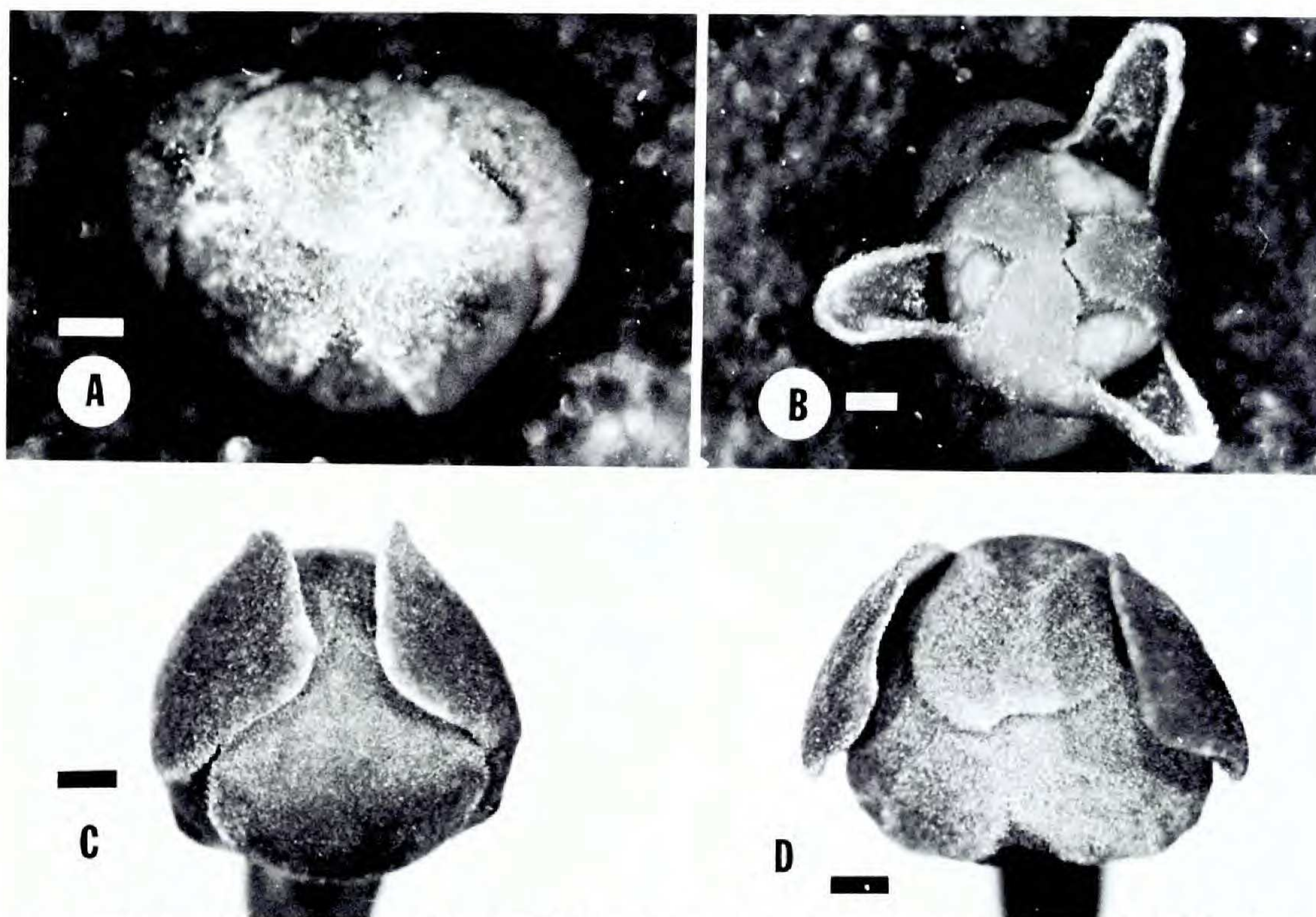


FIGURE 2. Petal aestivation in buds from *Polyalthia hypoleuca* complex. A, B, *P. glauca* (Rogstad 939): A, outer petals not substantially overlapping; B, inner petals not substantially overlapping (outer ones pulled back). C, D, *P. discolor* (Rogstad 814): C, outer petals slightly overlapping; D, inner petals significantly overlapping (lower outer one removed). Scale bars = 1 mm.

the purposes of this investigation, the most prudent approach is to maintain the group within *Polyalthia* until the needed reclassification is attempted. The implications of the above taxonomic problems when using congeneric species to investigate the problem of closely related, sympatric species are explored below.

Sinclair (1955, and references therein) followed most previous researchers in dividing the genus into two sections, *Eu-Polyalthia* Blume (or, by later convention, *Polyalthia*), defined as those species with two or more ovules per carpel, and *Monoon* Miq., comprising those with only one. Sinclair further suggested that distinct species groups existed within each section but did not explicitly propose character suites by which they could be distinguished. Examining these groups as candidates for a monophyletic group with sympatric species, I determined from herbarium and field work that one complex of species, the *P. hypoleuca* complex, was especially suitable in that a unique suite of characters is shared by all the members of the group and various members were found growing sympatrically at different field sites. My final concept of this complex, although related to Sinclair's Group 1 of sect. *Monoon* (1955; he included only *P. sumatrana* (Miq.) Kurz, *P. hypoleuca* Hooker f. & Thomson, *P. glauca*, *P. longifolia* (Sonn.) Thwaites, and *P. parkinsonii* Hutch.), is quite different from his as to both the limits of the group and the circumscriptions



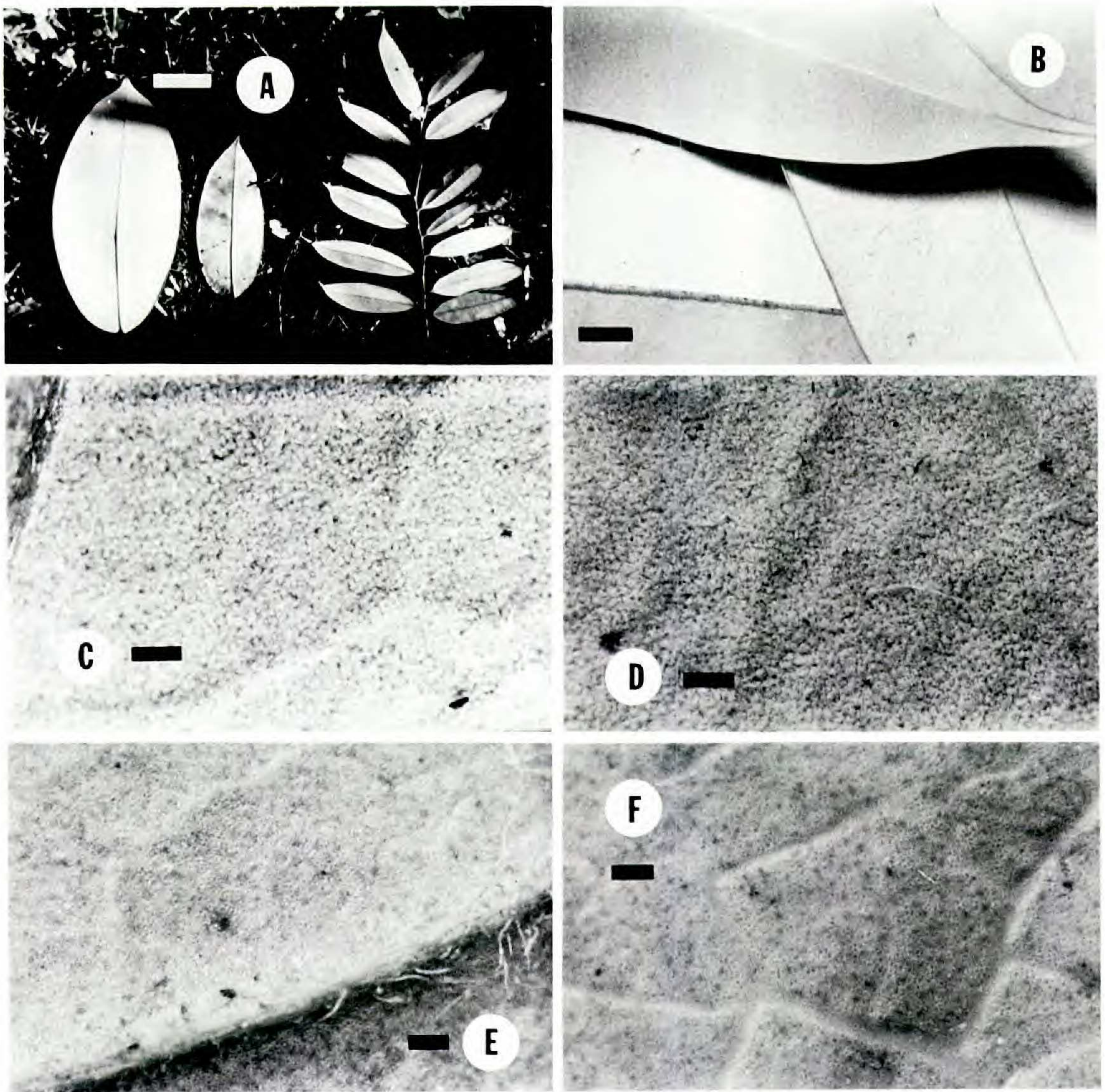


FIGURE 3. Leaves. A–D, species of *Polyalthia hypoleuca* complex (note weak secondary venation and uniformly white abaxial surfaces): A, *P. ovalifolia* (left; Rogstad 843) and *P. hypoleuca* (right; Rogstad s.n., 19 Dec. 1983), scale bar = 5 cm; B, 3 species sympatric at Pasoh Forest Reserve, peninsular Malaysia (*P. hypoleuca* above, *P. sumatrana* lower right, *P. glauca* lower left), scale bar = 0.5 cm; C, *P. glauca* (FRI 27582), uniformly distributed papillae, scale bar = 0.5 mm; D, *P. multinervis* (Rogstad 813), uniformly distributed papillae, scale bar = 0.5 mm. E, F, abaxial surfaces representative of *Polyalthia* species not in *P. hypoleuca* complex (note absence of dense, uniformly distributed papillae): E, *P. cauliflora* (Nur 18585); F, *P. insignis* (Hooker f.) Airy-Shaw (SAN A 4325); scale bars = 0.5 mm.

of the species within it. Nevertheless, Sinclair was probably segregating his Group 1 by implicitly recognizing some of the characters by which I explicitly delimit the *P. hypoleuca* complex here.

#### THE LIMITS OF THE POLYALTHIA HYPOLEUCA COMPLEX

I include in the *Polyalthia hypoleuca* complex only those species with all of the following seven characters: densely and uniformly distributed papillae cov-



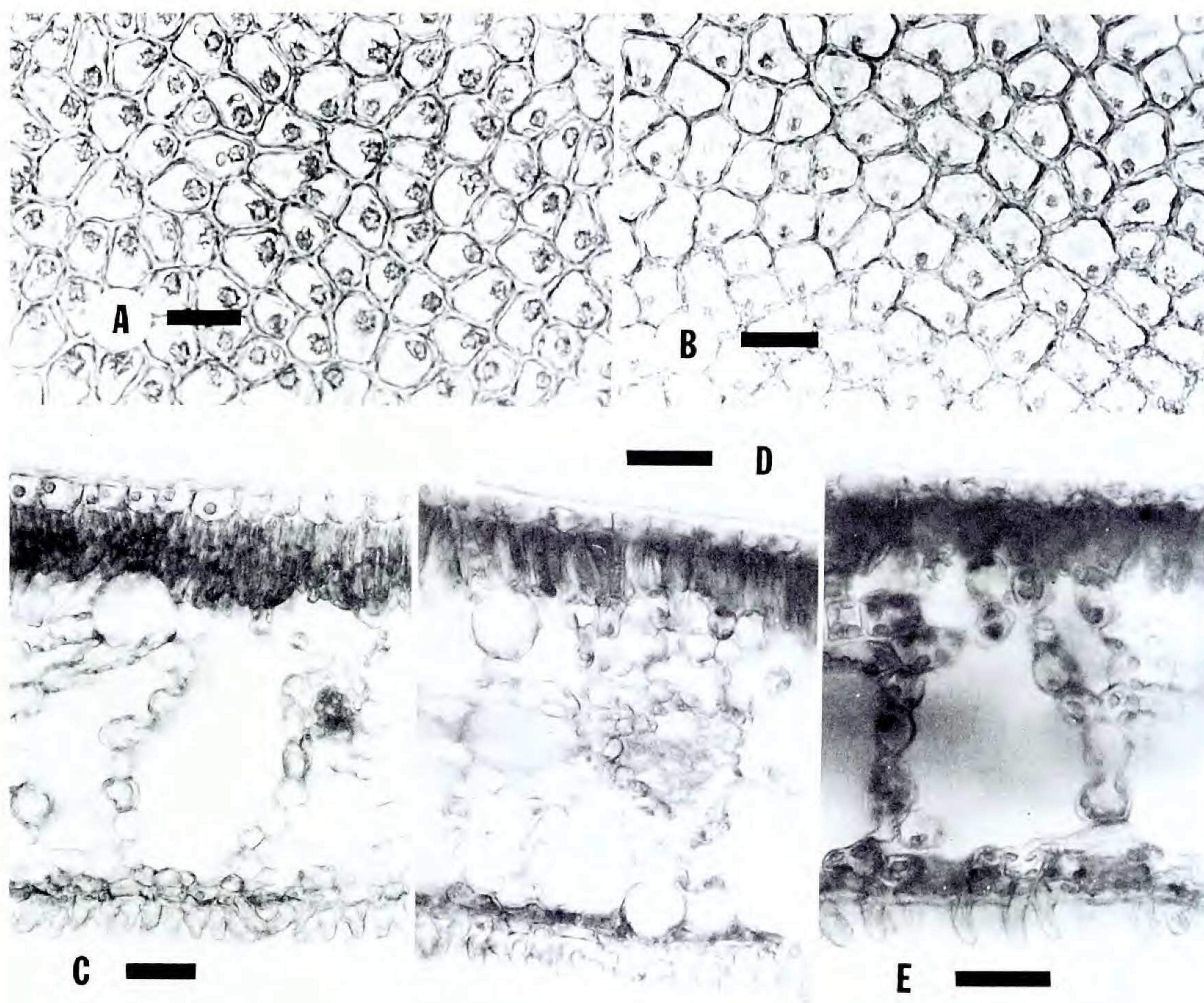


FIGURE 4. Features of leaf anatomy shared by all members of *Polyalthia hypoleuca* complex. A, B, epidermal peels showing thickened anticlinal walls: A, *P. sumatrana* (Rogstad 508); B, *P. discolor* (Rogstad 814). C–E, cross sections showing abaxial papillae: C, *P. glauca* (Rogstad 939); D, *P. sumatrana* (Rogstad 508); E, *P. multinervis* (Rogstad 813). Scale bars = 30  $\mu$ m.

ering the abaxial surface of leaves; extremely thin secondary veins differing little in diameter from the tertiary ones; secondary veins usually not forming a strong or relatively straight intramarginal vein, and relatively more numerous and closer together than in most taxa of the family; fundamentally white bark; monosulcate, “boat-shaped” pollen; pollen-wall architecture including a psilate, moderately perforated tectum, regular columellae, and a bipartite, foliated basal layer (Rogstad & Le Thomas, in prep.); and spiniform endosperm ruminations.

The most easily recognized of these characters is the densely and uniformly distributed papillae on the abaxial surface of the leaves (FIGURES 3, 4C–E). These papillae, which are lacking in all other species of *Polyalthia* (see, for example, FIGURE 5), cannot be seen readily with a 10 $\times$  hand lens, and so the use of a dissecting microscope (at least 25 $\times$ ) is recommended. It is probably the dense distribution of these papillae that colors the lower leaf surfaces of all species in this group white (often mixed with pale green, brown, gray, or gold). While several genera of this family (e.g., the *Dasymaschalon* Dalla Torre &



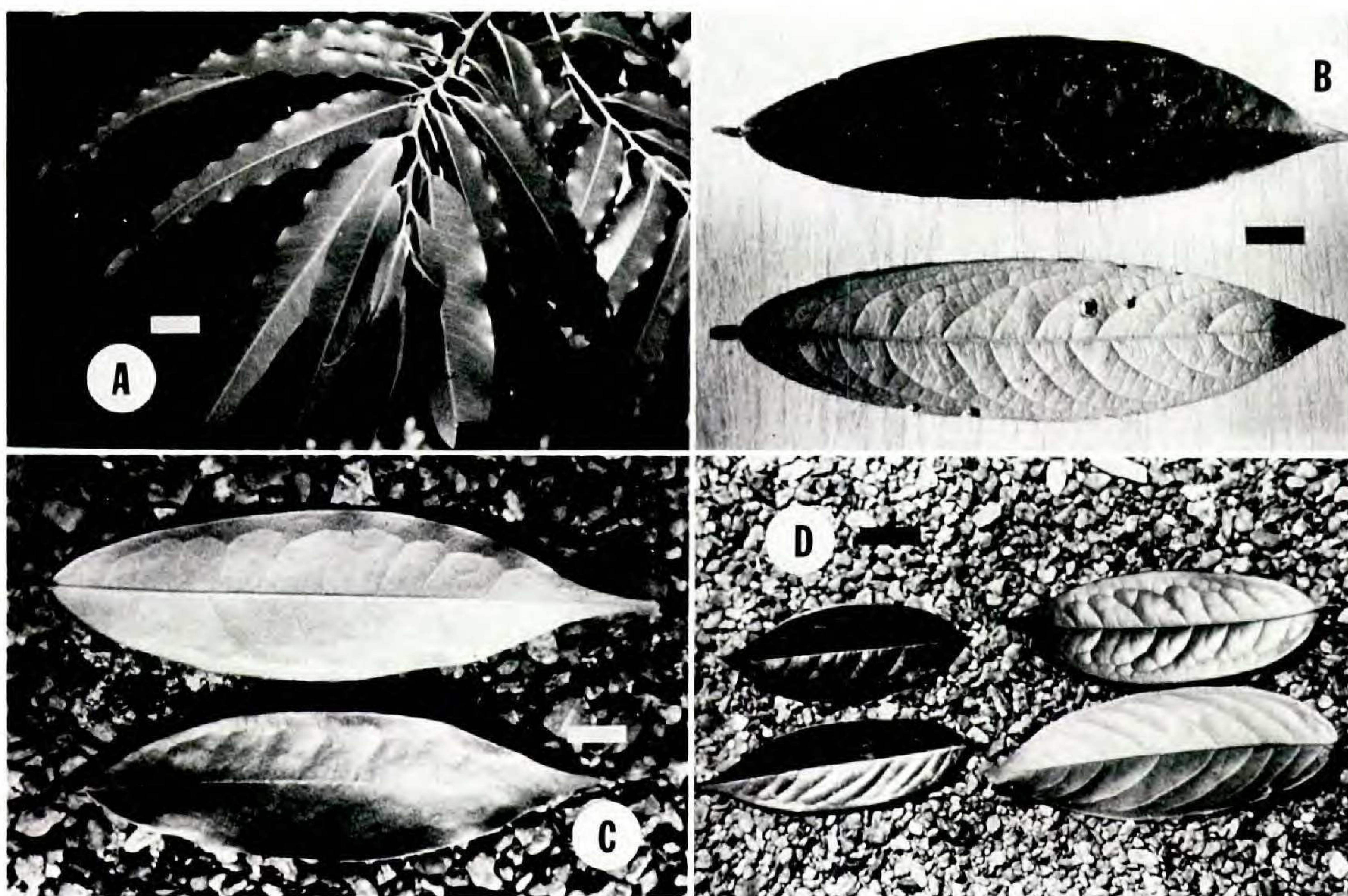


FIGURE 5. Leaves from *Polyalthia* species not in *P. hypoleuca* complex (note strong secondary venation): A, *P. longifolia* (Rogstad 960), scale bar = 2 cm; B, *P. cinnamomea* (Rogstad 936), scale bar = 2 cm; C, *P. cauliflora* (Rogstad 951), scale bar = 1 cm; D, *P. rumphii* (above; Rogstad 922) and *P. jenkinsii* (below; Rogstad 956), scale bar = 3 cm.

Harms-*Desmos* Lour. complex; some species of *Friesodielsia* Steenis, *Popowia* Endl., and *Xylopia* L.) have at least a few species with white abaxial leaf surfaces, most lack papillae, so this color must be caused in the latter genera by some other feature of the abaxial surface, for example, the nature of the waxy cuticle.

As far as I am aware, with the possible exceptions discussed here and below, leaf papillae of similar distributional uniformity, density, and structure are not found regularly in any other taxa of the Annonaceae. Roth (1981; pers. comm.) has indicated that within the family, the papillae most similar to those of the *Polyalthia hypoleuca* complex are found in *Onychopetalum* R. E. Fries, *Bocageopsis* R. E. Fries, *Richella* A. Gray, *Rollinia* St. Hil., *Ruizodendron* R. E. Fries, and *Woodiella* Merr. I have examined the holdings of these taxa (see APPENDIXES 1, 2) at A, GH, MO, and US, and in none have I seen leaf papillae identical in form or distribution to those found in the *P. hypoleuca* complex. Further, all of these taxa are quite different in floral and fruit morphology from members of the complex; only *Woodiella* is also an Old World genus. In a survey of 38 Neotropical genera, Van Setten and Koek-Noorman (1986) reported papillae for at least some species in *Bocageopsis*, *Ephedranthus* S. Moore, *Onychopetalum*, *Ruizodendron*, *Annona* L., and *Rollinia*. However, a comparison of their description of the papillae and their figs. 4 and 9 with FIGURE 4 here demonstrates differences in papilla structure and distribution between members of the *P. hypoleuca* complex and all of the genera they listed. Still,



further investigations of the distribution and taxonomic importance of abaxial leaf papillae in the genera noted by Roth, as well as by Van Setten and Koek-Noorman, are needed. While none of the members of these genera has all seven of the characters defining the *P. hypoleuca* complex, and all share with their congeners numerous characters not found in the complex, some of these species are worthy of consideration in the search for possible outgroups to the complex.

Of all the characters setting the *Polyalthia hypoleuca* complex apart, those relating to leaf venation are the most difficult to describe because occasionally only subtle differences exist between members of the complex and other species. Rarely, no differences are readily apparent. Thus, these characters are best examined in direct comparisons between specimens. First, the secondary veins are very fine and differ little in diameter from the tertiary ones, while in most Annonaceae they are much broader. In the *P. hypoleuca* complex, veins of both degrees are only very slightly raised above the leaf surface and are often difficult to see. Second, the secondary veins do not usually form a strong or relatively straight intramarginal vein, and they are relatively more numerous and closer together than in most taxa of the family. The vein characters of the *P. hypoleuca* complex can be compared with those of other representative species of the genus in FIGURES 3 and 5.

The bark of species of the *Polyalthia hypoleuca* complex is a rare type in the family in that it is fundamentally white (FIGURE 6), although especially on the young twigs and branches it may be tinted with shades of yellow or red in some species. I have been unable to find identical bark coloration in any other species of the genus, or even within the family (e.g., see Sinclair (1955); pers. obs.), with the following exceptions. White bark has been noted for *Pseudoxandra cuspidata* Maas (although brown bark also occurs in this species) and in *Oxandra leucodermis* (Spruce) Warm., apparently the only two known Neotropical species with this characteristic (Maas *et al.*, 1986).

Another character uniting the species of the *Polyalthia hypoleuca* complex was first noted by Walker (1971). In his survey of annonaceous pollen types, he placed *Polyalthia* in his tribe Uvarieae, which consists of those taxa with solitary, inaperturate, radiosymmetric pollen. He noted, however, that of the 22 species examined, *P. glauca* and *P. hypoleuca* stood apart in having sulcate, "boat-shaped" pollen. All of the taxa in the *P. hypoleuca* complex have pollen that is indistinguishable from that of these two species (Rogstad & Le Thomas, in prep.). I have also examined the pollen of four other Malesian species of *Polyalthia* (i.e., *P. lateriflora* (Blume) King, *P. obliqua* Hooker f. & Thomson, *P. sclerophylla* Hooker f. & Thomson, *P. socia* Craib; Rogstad 931, 935, 930, and 958, respectively) not treated by Walker; none of these species has pollen of the type found in the *P. hypoleuca* complex (see also Le Thomas, 1988). Walker (1971) found that sulcate, boat-shaped pollen was extremely rare in the Old World, occurring only in the genus *Enantia* Oliver of Africa and the two species of *Polyalthia* noted above. Walker did find such pollen in ten Neotropical genera, and these along with *Enantia* constitute his tribe Malmeae. Le Thomas (1981) has also found this pollen shape in a few other African genera and, more importantly here, in at least seven species of *Polyalthia* from



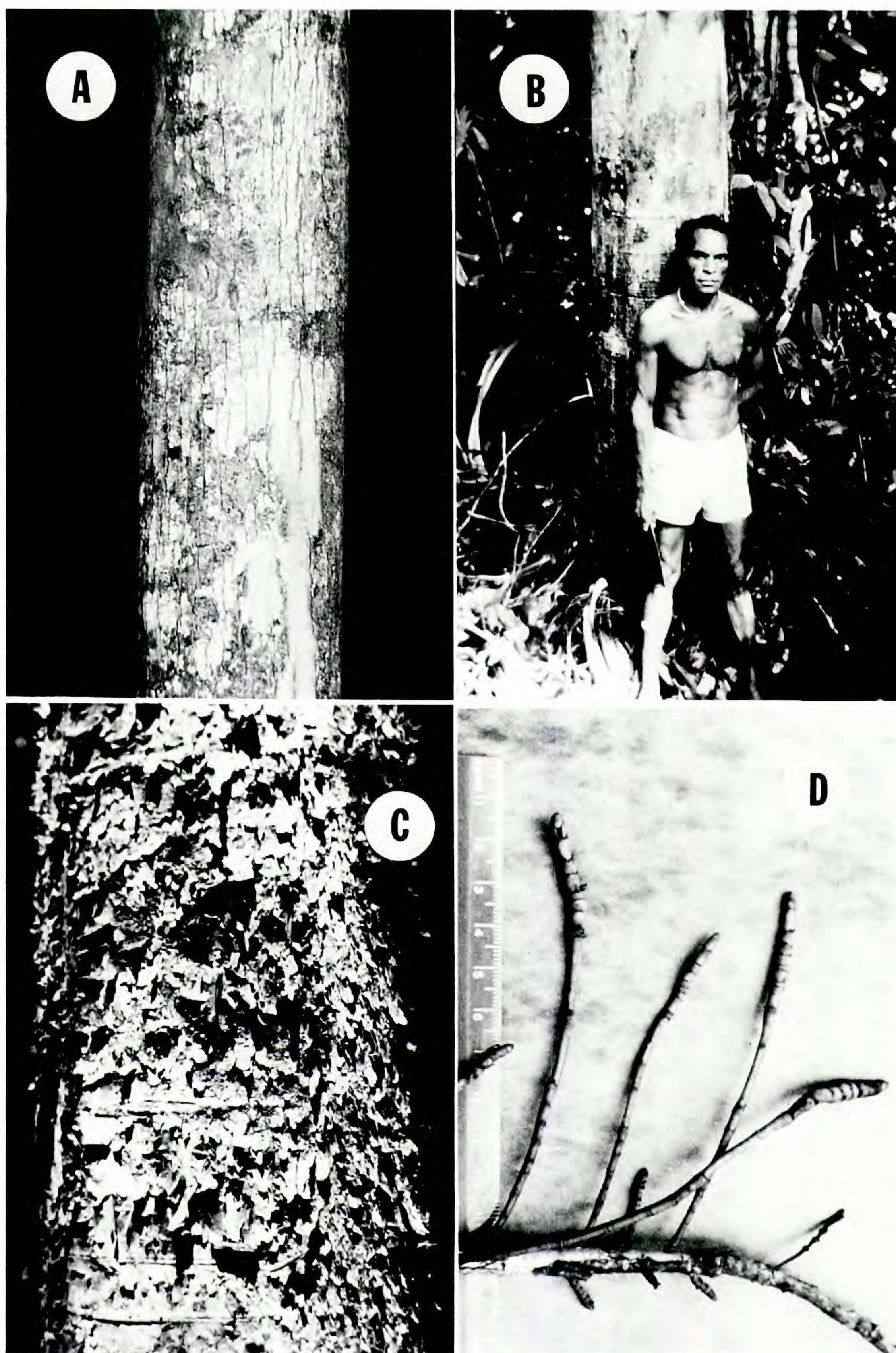


FIGURE 6. A–C, bole characters in *Polyalthia hypoleuca* complex: A, *P. hypoleuca* (79 cm girth at breast height), fissured bark lacking hoop marks; B, *P. discolor* (123 cm girth at breast height), smooth bark with horizontal hoop marks; C, *P. glauca* (104 cm



Africa and Madagascar. It should be noted that Gottsberger and Silberbauer-Gottsberger (1984) have cautioned that the apparent pollen shape of some Annonaceae may be an artifact of preparation.

Another feature that indicates a close genealogical relationship among the species here included in the *Polyalthia hypoleuca* complex is the architecture of the pollen wall (Rogstad & Le Thomas, in prep.). The five species of the complex for which pollen-wall examinations have been possible have a psilate, moderately perforated tectum, with regular columellae and a bipartite, foliated basal layer. While pollen appropriate for TEM observation of this feature has not yet become available for the sixth member of the complex (*P. ovalifolia* S. H. Rogstad), observations by compound microscope indicate that it agrees in external tectal construction with that from other members here included in the complex. This type of pollen architecture appears to be rare in the family; *Enantia chlorantha* Oliver (Le Thomas, 1981) and *Ephedranthus amazonicus* R. E. Fries (Waha, 1985), both placed by Walker in his tribe Malmeae, are the only examples thus far known from outside of the genus. The majority of the numerous other Annonaceae examined have a different surface architecture (Walker, 1971; Le Thomas, 1981; Waha, 1985; pers. obs.). Within *Polyalthia*, Le Thomas (1981) has described a pollen-wall architecture very similar to that of the species of the *P. hypoleuca* complex for *P. capuronii* Cav. & Keraudren, *P. emarginata* Diels, *P. heteropetala* Diels, and *P. oligosperma* (Danguy) Diels, all from Madagascar.

A final character that unites the members of the *Polyalthia hypoleuca* complex concerns the nature of the endosperm ruminations. All Annonaceae have endosperm that is divided by "ruminations as transverse folds of the tegmen or, also, of the testa or middle integument" (Corner, 1976, p. 68). In cross section the seeds have ruminations that can be a) very regular and platelike with a central "cross" of endosperm (Corner, 1949, fig. 12A; FIGURE 7C); b) irregular as though the regular plates just mentioned are broken into pieces of various sizes and distributions (Corner, 1949, fig. 14D, E; FIGURE 7D); or c) numerous, very fine, and needlelike (spiniiform; FIGURE 8A, B). The endosperm ruminations of most of the annonaceous species that have been described in the literature are type a or b (e.g., Corner, 1949, 1976; Periasamy & Swamy, 1961; Rao, 1975, 1979, 1982), while those of all of the species here included in the *P. hypoleuca* complex are spiniiform. Outside of the genus *Polyalthia*, spiniiform ruminations have been found in *Bocageopsis*, *Crematosperma* R. E. Fries (not all species), *Enantia*, *Onychopetalum* R. E. Fries, *Oxandra* A. Rich. (not all species), *Piptostigma* Oliver, *Polyceratocarpus* Engler & Diels, *Popowia* Endl., *Pseudoxandra* R. E. Fries, *Pseuduvaria* Miq., *Richella* A. Gray, and *Unonopsis* R. E. Fries (see APPENDIX 1).

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girth at breast height), mature tree, flaking white bark with red bole beneath (note hoop marks). D, *P. glauca*, distal portion of emergent pneumatophore (note annular scars indicating rhythmic extension growth).



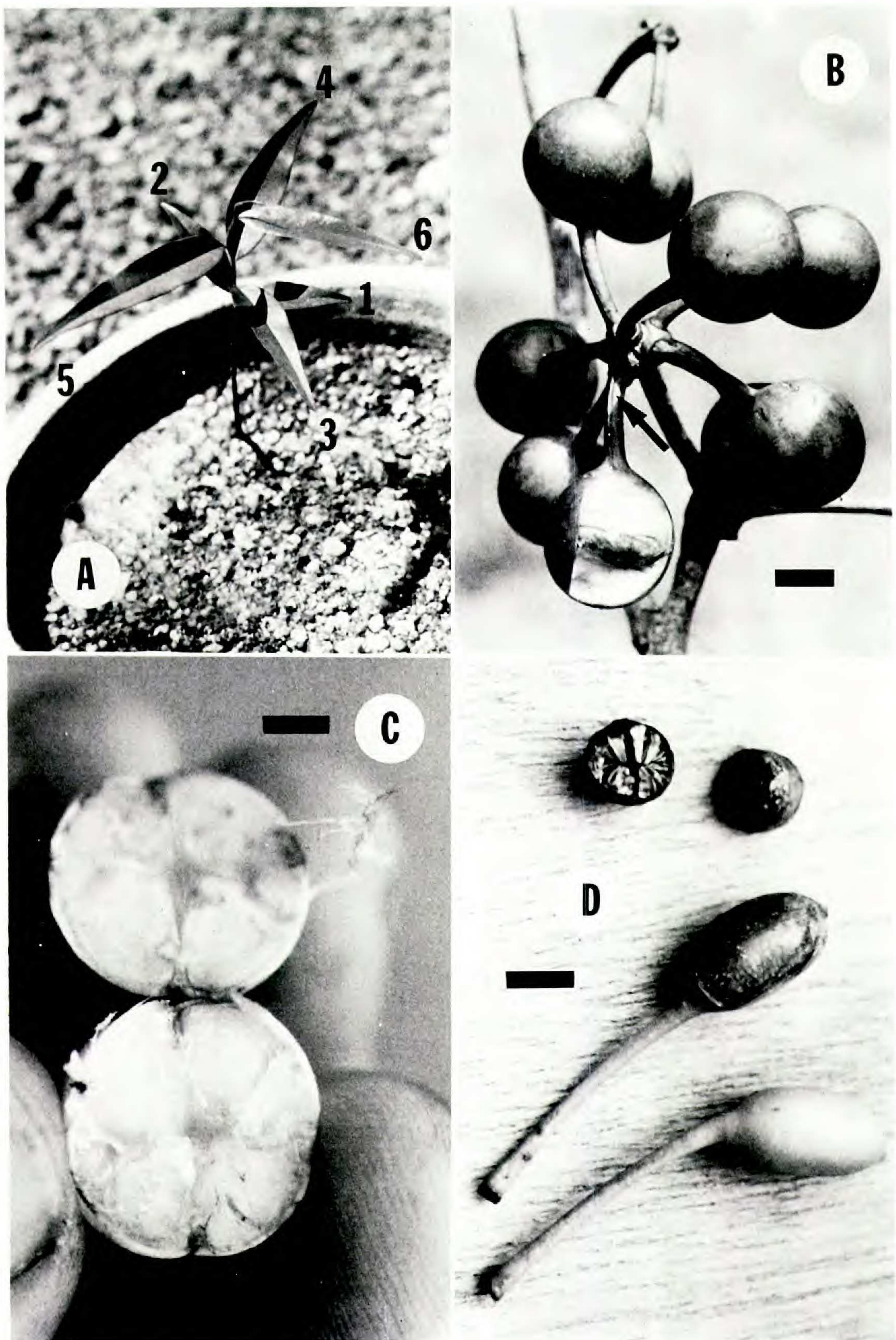


FIGURE 7. Seedling, fruits, and seeds: A, *Polyalthia hypoleuca* seedling, mature leaves numbered in order of development; B, *P. discolor* (Rogstad 814), mature fruits, micropylar region of seed exposed indicating ventral orientation of seed (arrow indicates



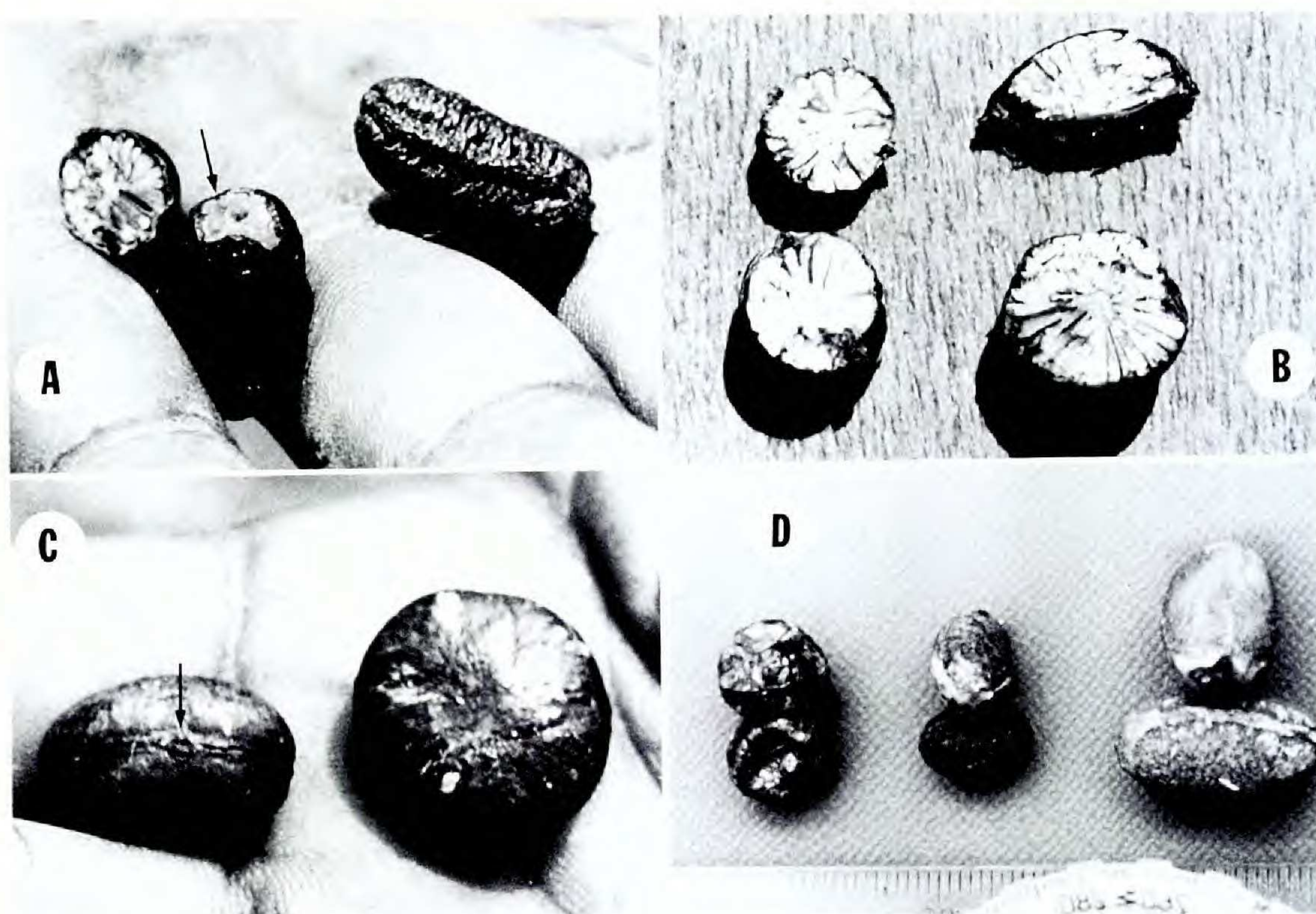


FIGURE 8. Seeds of *Polyalthia hypoleuca* complex: A, *P. multinervis* (Rogstad 813), ellipsoid, with spiniform endosperm ruminations, pronounced aril scar (arrow), and circumferential ridge; B, *P. sumatrana* (Rogstad 508), sections at various levels, showing spiniform endosperm ruminations throughout; C, *P. discolor* (Rogstad 814), regular, lozenge shaped, circumferentially grooved, lacking pronounced aril scar at micropylar region (arrow); D, *P. glauca* (left; Rogstad 939), *P. hypoleuca* (center; Rogstad 912), *P. sumatrana* (right; Rogstad 508).

I have also examined species from over 24 additional genera of Annonaceae (including 34 species of *Polyalthia*, and all genera now known to share at least one other character from the suite defining the *Polyalthia hypoleuca* complex) for this character (see APPENDIX 1). Seeds with exclusively needlelike ruminations were lacking in these other genera but were found in *P. oliveri* Engler & Diels, *P. stuhlmannii* (Engler) Verdc., *P. suaveolens* Engler & Diels, *P. suberosa* (Roxb.) Thwaites, *P. capuronii*, and *P. oligosperma*. Of these species, only the latter two have as many as three of the seven characters I use to delimit the complex, a finding discussed further below. Although wider surveys of this seed character are needed, the above evidence indicates that the spiniform endosperm ruminations found in all of the species of the *P. hypoleuca* complex can be included in the suite of characters distinguishing this group.

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“stigmatic crest” remnant on stipe), scale bar = 1 cm; C, *P. longifolia* (Rogstad 960), cross section of mature seed, scale bar = 3 mm; D, *P. jenkinsii* (Rogstad 956), near-mature carpels and seed, scale bar = 5 mm.



Another character deserves mention as a potential member of the suite defining the *Polyalthia hypoleuca* complex. A survey of the leaf anatomy of several species of the genus has revealed that all species of the complex have an adaxial epidermis in which all or most cells have straight, thickened anticlinal walls (FIGURE 4A, B). In this survey 34 other species from the genus were examined for this character (see APPENDIX 2); it was lacking in all but two of them. These results contrast with the findings of Van Setten and Koek-Noorman (1986), who found similar-looking adaxial epidermis in several taxa, which they did not list. These authors suggested that the anticlinal walls appear thickened due to "thickened cuticular ledges following the anticlinal . . ." walls (p. 22; see *figs.* 6, 7). With the species of the *P. hypoleuca* complex, it is not clear whether thickened ledges or thickened anticlinal walls give rise to this effect (see FIGURE 4C). While this character is not common in *Polyalthia*, its distribution in the rest of the family is unclear, so it cannot yet be included in the list of characters defining the complex. Interestingly, the only other two species of *Polyalthia* found to have an adaxial epidermis similar to that seen in all members of the *P. hypoleuca* complex are from Africa, and one of these, *P. oligosperma* (Dangy) Diels, is a leading potential candidate as an outgroup species for the complex.

In summary, a unique suite of seven characters is shared by all and only the members I am placing in the *Polyalthia hypoleuca* complex. Although these characters are uncommonly found in other taxa of the family, each usually occurs in relative isolation from the other characters. A detailed analysis of the distribution of these characters outside of the *P. hypoleuca* complex has been conducted (Rogstad & Le Thomas, in prep.), and only an outline of the resulting conclusions regarding the monophyly and taxonomic position of the complex is given here. Within *Polyalthia*, only *P. capuronii* and *P. oligosperma* (both from Madagascar) have as many as three of the seven characters, making them the best congeneric choices as possible sister lineages to the *P. hypoleuca* complex. Outside of the genus, it is interesting that the seven characters find their densest distribution in a group of eleven genera designated by Walker (1971) as tribe Malmeae. Of these, one African and four Neotropical genera have species possibly possessing three of the seven characters, while only the Neotropical genera *Oxandra* and *Pseudoxandra* have species perhaps possessing as many as five, making these latter species the most likely choices as sister taxa to the complex. Note that all of the species having more than two of the seven characters are from Africa/Madagascar or the Neotropics, giving strength to the notion that at the least, the members of the *P. hypoleuca* complex are the only Asian-Oceanic members of a larger monophyletic group with other members occurring in other areas. Further, all of the taxa noted above as having at least one of the seven characters share with their congeners characters not found in the *P. hypoleuca* complex (Rogstad & Le Thomas, in prep.). The latter finding, together with the fact that the character suite discussed above is found only in all members of the *P. hypoleuca* complex, leads to the conclusion that, by parsimony, the *P. hypoleuca* complex either is a monophyletic group (Rogstad & Le Thomas, in prep.) or is composed of all the Malesian members of



a larger, small monophyletic group with complementary members in Africa or the Neotropics.

#### TAXA EXCLUDED FROM THE POLYALTHIA HYPOLEUCA COMPLEX

One group of species, treated by Sinclair (1955) as members of the genus *Melodorum* Lour., is problematic because they bear abaxial leaf papillae most similar to those of the *Polyalthia hypoleuca* complex. In his survey of leaf papillae, Roth (1981; pers. comm.) did not see a close similarity between the papillae in *Melodorum* and those of the *P. hypoleuca* complex. The placement of *Melodorum* is contested (e.g., see Okada & Ueda, 1984), and various authors have described some of the relevant taxa as species in *Polyalthia* (including *P. aberrans* Maingay ex Hooker f. & Thomson, *P. aberrans* Pierre ex Finet & Gagnep., *P. affinis* Teysm. & Binnend., *P. diospyrifolia* Pierre ex Finet & Gagnep., and *P. siamensis* Boerl.).

While this is not the place to discuss in detail the proper placement of *Melodorum*, in my opinion these species differ from the genus *Polyalthia* because they are climbing shrubs, the sepals are connate, the petals are thick and coriaceous, with the inner ones distinctly smaller than the outer and not spreading as in *Polyalthia* (see Sinclair, 1955), and the chromosome number ( $2n = 16$ ) has not yet been found in *Polyalthia* (Okada & Ueda, 1984; Rogstad, unpubl. data). Further, although the papillae of some of the specimens of *Melodorum* are similar to those found in the *P. hypoleuca* complex (sheets that are clearly *Melodorum* according to the characters listed below are occasionally annotated as *P. glauca*), they are less dense and are only sometimes present. Additionally, the species of *Melodorum* (as denoted by Sinclair, 1955, for example) differ from all the species I assign to the *P. hypoleuca* complex in having very distinct leaf venation with an intramarginal vein well removed from the leaf margin, deeply grooved stigmas, globose pollen (Walker, 1971), and platelike endosperm ruminations. In light of these considerations, I conclude that little justification exists for including the taxa of Sinclair's *Melodorum* in *Polyalthia* or the *P. hypoleuca* complex, and that any similarity between their abaxial leaf papillae is of dubious value in trying to establish a close phylogenetic relationship between them.

*Polyalthia longifolia* must also be considered for inclusion in the complex. Although Sinclair (1955) placed this species in his Group 1, several lines of evidence argue against it. As noted above, Sinclair did not explain criteria for group inclusion, so I cannot address his reasons for the placement of *P. longifolia*. However, the species has not one of the seven character states listed above that I am using to define the *P. hypoleuca* complex (e.g., see FIGURES 5A and 7C, and Rao (1979)). Further, the staminate and carpellate portions of the torus in *P. longifolia* are pubescent, a character altogether lacking in any of the members of the *P. hypoleuca* complex. I would include *P. longifolia* in Sinclair's Group 6 because it has a pubescent torus, midribs deeply grooved longitudinally on the abaxial surface of dried leaves, platelike endosperm ruminations with a "cross" of endosperm clearly visible, the outer seed-coat surface



marked with parallel fine striations running perpendicular to the circumferential ring of the seed, and the first above-ground growth of the germinating shoot deriving from extension of the first internode above the cotyledons rather than from the hypocotyl (the latter being the case for all members of the *P. hypoleuca* complex).

Species that other authors recognize but that I have reduced to synonymy under other species within the *Polyalthia hypoleuca* complex are discussed below.

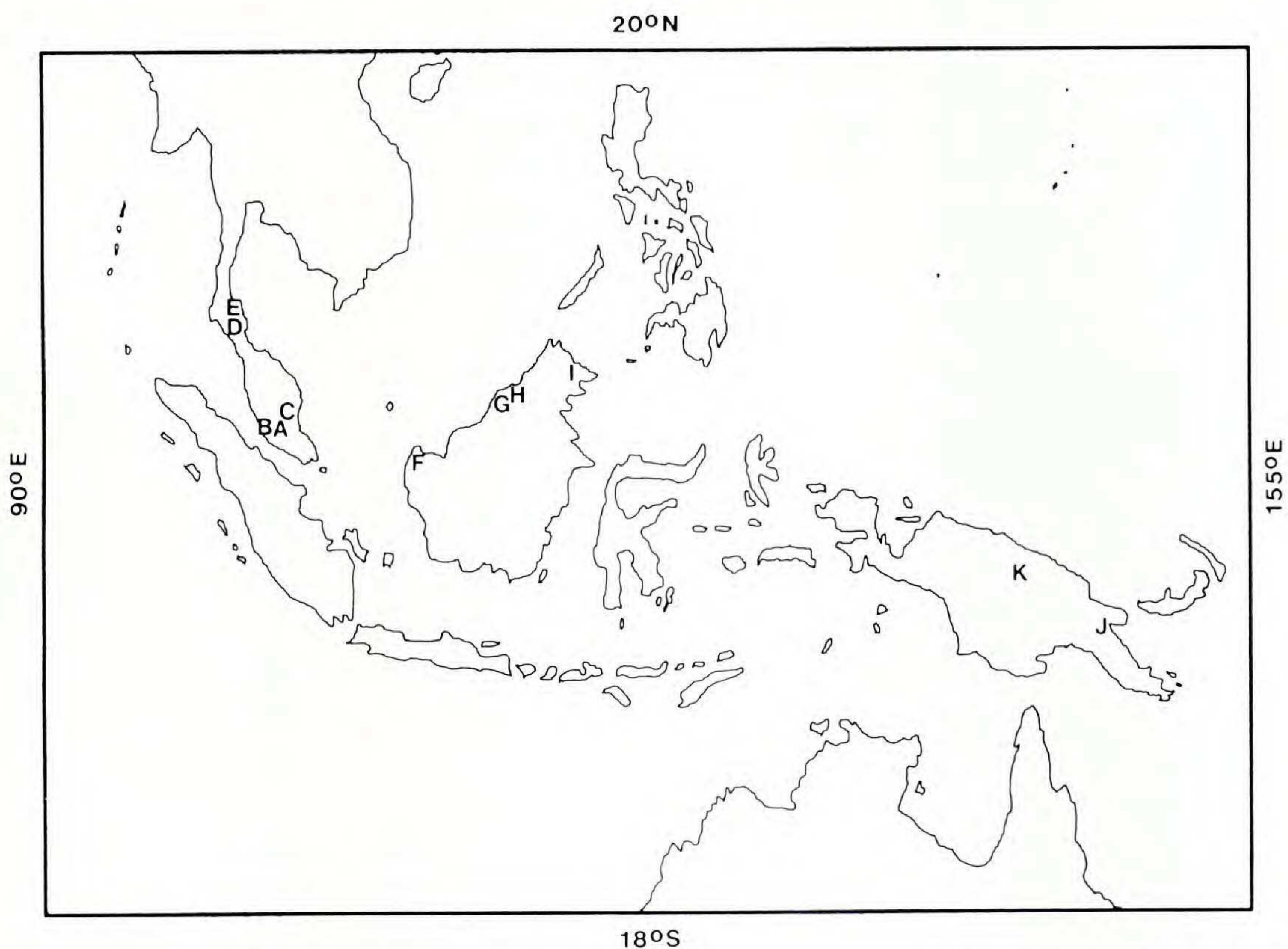
#### SPECIES CONCEPT

While it is not my purpose here to discuss the nature of species, it is important that I provide the working definition I have employed to define the species of the *Polyalthia hypoleuca* complex. My species decisions have been made primarily on a morphological basis: are there clear discontinuities by which species can be delimited? I have searched for such discontinuities by recording data on numerous characters from both herbarium and living specimens and then analyzing these data in several different ways, as outlined in the methods section below. Clear discontinuities were found in character-state distributions, and these form the basis for my species concepts. For two cases where these discontinuities are relatively slight, and in fact for all of the species discussed, the decisions reached here will be supported in later articles detailing the comparative autecologies of these species. Thus, my species are defined not only on morphological considerations, but also on an assessment of whether or not they are likely to be isolated genetically or ecologically in nature. The reader interested in weighing the sum of all the evidence bearing on the taxonomic decisions presented here may wish to consult the subsequent articles. Ultimately, the species concept I have used in this treatment is perhaps most fully in accord with the "evolutionary" species concept of Simpson (1961, p. 153): "a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies." This is not to say that the evolutionary species concept is the preferred one for all plant species, but after considering all of the information bearing on species in the *P. hypoleuca* complex, I believe it to be the most applicable here.

#### METHODS

Morphometric analyses were used to search for evidence of morphological species. Character observations and measurements were taken both from herbarium specimens at A, BK, BKF, BO, F, GH, K, KEP, KLU, L, LAE, MO, P, PNG, SAN, SAR, SING, U, US, and Yezin (Burma) and from living specimens collected in several Malesian locations (see MAP 1). All of the herbarium specimens used in these analyses, as well as representative voucher specimens of species for which field measurements are analyzed (*Rogstad* numbers deposited at A), are noted in the specimen citations. An attempt has been made to include specimens covering the full range of character variability for each species. The known geographic range determined from herbarium specimens for each species of the *Polyalthia hypoleuca* complex is depicted in maps accompanying the species





MAP 1. Sites visited. Peninsular Malaysia: Pasoh Forest Reserve (A), Telok Forest Reserve (B), Tasek Bera Reserve (C). Thailand: Khao Chong Forest Reserve (D), Khao Tha Phet Forest Reserve (E). Sarawak: Bako National Park (F), Lambir and Niah national parks (G), Baram River Site (H). Sabah: Sandakan (I). Papua New Guinea: Aluki Village (J), April River (K).

descriptions; specimens from the entire known range of each species have been included in the morphometric analyses. Coverage of character variability and geographic distribution is thus most comprehensive for the better-collected species.

Measurements of herbarium specimens were recorded from all sheets bearing several intact flowers and/or any fruits and were made with a ruler or with a dissecting microscope fitted with an ocular micrometer when appropriate. The most mature flower or fruit present with all the relevant characters intact was measured. Flowers were denoted as mature or immature based on characteristics determined from field observations. For most of the species, petals of immature flowers are open and radiating, while those of mature ones are erect and closely parallel to the longitudinal axis of the flower (Rogstad, in prep. b). In *Polyalthia glauca* and probably *P. ovalifolia*, the outer petals are erect until they turn yellow-orange at maturity, then the distal portion bends outward to 30° or more. Petals were also designated as being mature if label data indicated that they were other than greenish. Fruits were deemed mature if they were at least as large as the smallest fruit of a species for which label data indicated fruit color as deep red to black; fruits of all these species achieve maximum



size while still green, turning black when mature a number of weeks later (pers. obs.). Specimens with only one or a few flowers were generally not measured for all characters unless the specimen was judged as crucial to the study (e.g., at the edge of a species range or bearing an unusual character). To avoid unusual phenotypic effects on measurement of leaf characters, an average-size leaf was subjectively chosen from each specimen. Pertinent herbarium label data were recorded for the specimens. The categories of data collected for each herbarium specimen and used variously in the morphometric analyses reported below are listed in APPENDIX 3. A copy of the full data set stored on double-sided, double-density, 5.25-inch diskettes utilizing MS/PC-DOS format has been deposited with Rogstad (1986) in the Botany Libraries of Harvard University. A copy can be obtained free on request, provided the user agrees to share the results of any analyses of these data with the author and sends a self-addressed, stamped envelope containing an appropriate diskette.

In the case of living specimens, tree heights were measured with a Suunto PM5/360PC Clinometer following the directions provided. The girth of trees at breast height (GBH) was measured at 1.5 m by tape measure and converted to diameter at breast height (DBH).

These data were analyzed by several different methods utilizing the SYSTAT (Wilkinson, 1984; in conjunction with an IBM PC-AT), SAS Version 5 (SAS Institute, Inc., Cary, North Carolina), and BMDP (Health Science Computing Facility, University of California, Los Angeles, California) statistical packages. The last two packages were used as available at the Washington University Computing Facilities, St. Louis.

While the univariate and bivariate analyses presented in the results section below are widely used and self-explanatory, my choice of multivariate techniques requires justification. As stated above, the species concept I develop with regard to the *Polyalthia hypoleuca* complex is based on morphological analyses. I begin, therefore, by searching for discontinuities in morphological characters, attempting to apply the widely held tenet that good taxa are best defined not on one character, but on a suite of them.

Patterns of variation within and among characters are often very complex. Sokal (1985) argued that many taxa are polythetic, that is, are groups that can be defined by a suite of characters, with some or all of the members lacking one or another character. The literature is replete with disputes over the proper classification of organisms, and these are testimony both to the complex nature of character variation among organisms and to the fact that each investigator carries personal biases into subjective decisions about the importance of conflicting characters. Sokal and Rohlf (1980) have demonstrated that different taxonomists achieve different subjective classifications based on the same set of taxa, but the differences are greatly reduced when investigators employ standardized morphometric analyses of explicitly coded character states (Sokal & Rohlf, 1970). The task for the taxonomist, then, is to search for nonsubjective signals of morphological discontinuity (at best based on several covarying characters) that rise above the noise of characters exhibiting more or less random variation.

A review of literature descriptions, and of the sorting and annotation of



herbarium specimens by previous researchers of taxa I have included in the *Polyalthia hypoleuca* complex, indicated that this assemblage was in need of revision due to complex character distributions that did not always result in congruent or stable taxonomic entities. I have used multivariate analyses as an aid in defining the taxa in this group based upon characters and techniques that are repeatable and explicit.

Several multivariate statistical techniques have been designed to search for patterns in complex character-state data sets. A review of plant taxonomists' use of these techniques (Duncan & Baum, 1981) indicates that cluster analysis has been the most widely employed. However, since the first step in my analysis is an attempt to demonstrate whether or not any groups (clusters) exist based upon character variation, and since cluster techniques always give clusters even if a random data set is used, searching for the possible existence of clusters with a method that always yields them seemed questionable. Here I used a two-step approach that does not necessarily sort specimens into groups, but rather summarizes the degree to which character states covary among specimens and then, if groups are detected, permits a statistical test of group membership for each specimen.

The first step was to examine the data matrix by principal-components analysis, or PCA (SYSTAT; Wilkinson, 1984). Reviews of PCA theory, methodological assumptions, and constraints can be found in most texts treating multivariate methods (e.g., Nie *et al.*, 1975; Neff & Marcus, 1980; and their references), and the following discussion is simplified for brevity. With PCA as utilized here, the raw data matrix—in this case measurements of a set of characters taken from herbarium specimens—is analyzed to derive its corresponding correlation matrix (a covariance matrix can also be used, but since this approach is strongly influenced by characters of larger size, only correlation matrices have been employed here). From this matrix, principal components (axes) are extracted that are descriptors, in serial fashion from greatest to least, of variance among character states across the specimen set. The first principal component is the axis with the maximum variance. The second component axis is derived in the direction of greatest variance orthogonal to the first one, and thus successive axes are computed until all the variance in the data set is accounted for. Each principal component is a mathematical equation (eigenvector) that includes a term for each character weighted by a coefficient commensurate to that character's contribution to the total variance of that component. Each specimen can be assigned a numerical value along each component (the character coefficient times the character value for each character of that specimen summed over all of its characters) that summarizes the degree to which its characters covary with the other specimens in characters that heavily influence each component.

Specimens more similar to one another in the ways their characters covary are thus placed in closer proximity along the principal components than are those that differ. If strong patterns of character covariance exist, these will be detected in the first three or four components, where the greatest degree of variance is accounted for, the later components accounting for very little of the total variance. If patterns of character distributions are more or less random,



then the first components will not explain much more variance than later ones. If all specimens are plotted for their scores on three components, specimens with similar patterns of character correlation are placed in groups in the principal-components space defined by the three components. Use of PCA enables one to search for groups defined by suites of (covarying) characters and, once the principal components are calculated, to identify the characters that contribute most to the differentiation of groups along any particular axis. As indicated above, groups defined by suites of characters are preferred over groups defined by only one.

Two further steps often taken in PCA analyses should be mentioned. First, once all of the data have been analyzed, characters with no high loadings on any component can be removed from the data matrix and the analysis recalculated. This eliminates characters that vary randomly with respect to strongly covarying characters and therefore contribute only "noise" to the analyses. Groups or loadings on remaining characters may thus be given clearer definition. While I have conducted this type of exploration with the data sets used here, removal of low-weighted characters did not significantly improve the results (and is a somewhat subjective decision in any case), so only results including all of the continuous characters are reported here. Second, once a set of principal components has been determined for a data set, the corresponding component axes can be rotated to search for more meaningful components by simplifying the component structure (Nie *et al.*, 1975). Although rotation may thus improve the interpretability of the component loadings, it did not in the examples discussed below, so only unrotated solutions are presented.

Note that PCA does not always give clear groups; decisions of group membership may be difficult and sometimes ultimately rest upon the discretion of the practitioner. As far as I am aware no method has yet been devised for PCA that permits a statistical test of the strength of groups or of group membership by individual cases.

When visual inspection of the PCA analyses of the *Polyalthia hypoleuca* complex data set resulted in hypotheses of groups of specimens, I utilized discriminant analysis (again, see standard texts on multivariate statistical techniques: e.g., Nie *et al.* (1975), Neff & Marcus (1980), and their references) to test the statistical strength of the membership of each specimen in the hypothesized group. The same data matrix as used above in the PCA can be analyzed by discriminant analysis techniques, although in the latter case each specimen must be designated, before the analysis is undertaken, as belonging to one of the hypothesized groups.

The specific technique used here is a jackknifed discriminant analysis, in which the first step is to remove one specimen from the data set. Next, a set of linear discriminant functions (axes) is derived, each maximizing, in decreasing order, the separation of the groups. In other words, the first function maximizes the separation of the groups, the second function is orthogonal to the first and is the next best function at maximizing group separation, and so on, until the maximum number of functions has been derived. If the members of the *a priori* groups are much more similar to one another than they are to members of other groups, their placement on a discriminant function axis



should cluster them in relative proximity on that axis away from other groups or specimens. As with PCA above, once the discriminant functions are calculated, the characters that contribute most to the differentiation of groups along any particular axis can be identified.

If a set of variables is found in the first three or four discriminant functions that provides satisfactory discrimination for the *a priori*-defined groups, then the excluded specimen can be statistically "classified" as to the group in which it belongs. This specimen is then returned to the total data set, and the next specimen in the data table is excluded and the above procedure repeated. In this way, each specimen can in turn be removed from the data set and then classified as to group membership in relation to the remainder of the specimens. If groups are well defined, all specimens should be correctly placed with high statistical confidence as belonging to the group to which it was assigned *a priori*. If no clear groups are present, many individuals will be assigned to groups other than those in which they were first placed as a result of the PCA analyses.

It is important to keep in mind that the species assignments indicated in all of the results below have been ultimately decided *a posteriori* with respect not only to the totality of the morphometric evidence presented here, but also with regard to ecological characteristics to be detailed in related articles (Rogstad, in prep. a, b).

A valuable feature of both PCA and discriminant analysis is that the percentage of the total variance or dispersion in the data set explained by each extracted principal component or discriminant function, respectively, is calculated. In a totally random data set, little underlying structure of correlation of variation of variables would be expected, so a particular principal component or discriminant function will not explain much more of this variance or dispersion than the one immediately following. However, if there is structure in the data, then at least the first principal components or discriminant functions derived should explain a disproportionately large portion of the variance or dispersion. In all of the results reported below, the latter possibility will be seen to be the case.

Another useful type of information obtainable from both PCA and discriminant analysis derives from the calculation of the component loadings and the coefficients for the canonical variables, respectively. These are informative as to which of the characters are most important with regard to the variance or dispersion explained by each principal component or discriminant function. Characters with larger loadings or coefficients on a principal component or discriminant function have patterns of correlated variation with regard to that component or function and can likely be used in suites of correlated characters that best define discontinuous groups (species).

Discriminant analysis and PCA are subject to certain constraints and restrictions. For example, both methods assume multivariate normality for the data. While PCA is thought to be robust against all but extreme deviations from normality (e.g., see Sneath & Sokal, 1973), discriminant analysis also includes the further assumption of equal variance-covariance matrices within groups (Neff & Marcus, 1980). However, use of discriminant analysis is not invalidated even when both assumptions are violated to some degree if errors



of classification are small (Neff & Marcus, 1980), which is the case for all the results presented below. Only characters that are continuous or meristic over broad ranges are included in the data matrices analyzed by PCA and discriminant analysis here. Those that are clearly not normally distributed (e.g., information, such as color, that is designated by arbitrary coding; presence-absence data) are not included in the PCA and discriminant-analysis results described below, although, as will be seen, such data can be used informatively in conjunction with these analyses. Each analysis also includes only specimens with no missing values for any character employed. Additionally, both the principal components and the discriminant functions of the respective methods are based on linear models, and for present purposes this approach has been accepted. Finally, the species treated here have not been equally well collected, and therefore the sample sizes are not equal. While this is not a major problem for PCA, it can affect discriminant analysis. Thus, in the results reported here, all discriminant analyses were performed with the BMDP option PRIOR adjusted to reflect the sample size of each species.

Obviously, the ideal statistical requirements of these methods are only at best approached, rather than met entirely, in the analyses discussed here. This will probably always be the case for systematists' data sets due to the problems inherent in collecting biological information. Does this indicate that these tests should not be utilized? I maintain that they should be used as exploratory and descriptive tools. The results detailed below are not presented as incontrovertible systematic truth, but rather as aids that influenced my taxonomic decisions. Further, the characters, methods, and decisions are explicit and repeatable, and other workers can follow the development of concepts, modify the analyses, or contribute additional information in a prescribed manner. At the very least, the presentation of systematic analyses by these methods is heuristic in rapidly conveying to the reader not only the extremes of variation important in defining groups (the usual information provided in systematic treatments), but also the degree to which variation exists within each group. For example, after PCA of the character matrix, data for any desired character are separately available for statistical analysis within selected groups. Graphic depictions of the distribution of individuals according to their scores on various components provide rapid understanding of their dispersion, due to the covariance of the characters heavily weighted on those components.

## RESULTS

Since over 50 characters from 172 flowering specimens and 16 characters from 230 fruiting specimens were recorded, it would be inefficient to reproduce all of the possible permutations of uni-, bi-, tri-, and multivariate character analyses here. Instead, only a few representative examples will be presented.

In the graphic presentation of these results, the species designations have been made after consideration of all of the data and analyses presented here and in subsequent related articles (Rogstad, in prep. a, b). In an evaluation of only two or three characters, a few specimens of a species may exhibit character states of another species for any (or rarely all) of them, but they otherwise



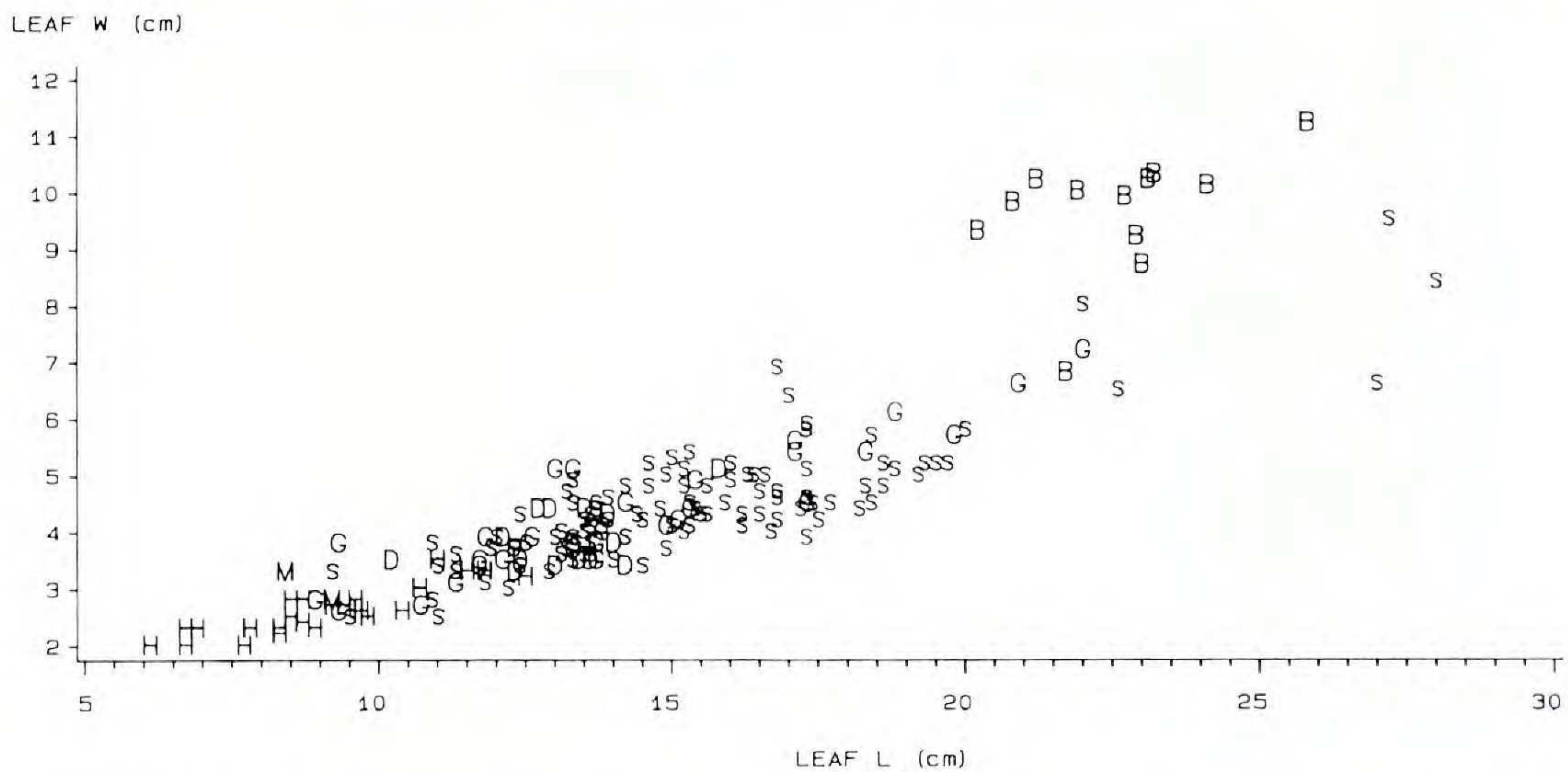


FIGURE 9. Leaf length vs. width for specimens of *P. hypoleuca* complex: B = *P. ovalifolia*, D = *P. discolor*, G = *P. glauca*, H = *P. hypoleuca*, M = *P. multinervis*, S = *P. sumatrana*.

conform with the species to which I have assigned them. It will be seen from a comparison of the following bivariate and multivariate analyses that a systematist giving more weight to certain characters than others (as judged from bivariate comparisons) may arrive at different conclusions than those reached by multivariate analyses.

Sinclair (1955) noted that although leaves of *Polyalthia sumatrana* and *P. glauca* are nearly indistinguishable, those of *P. hypoleuca* are smaller and have closer veins. However, as is shown in FIGURE 3B, there is some overlap of specimens assigned to both *P. sumatrana* and *P. glauca* with *P. hypoleuca* with respect to leaf size. This is not to say that there are not tendencies in leaf sizes of these species, but this overlap negates leaf size as a simple character by which these species can be delimited absolutely. In fact, if one examines each data point in FIGURE 9, disregarding the species designations that have been made based on the sum of the vegetative, floral, fruit, and ecological data, it is difficult to define distinct groups, except perhaps one comprising specimens of *P. ovalifolia* and another composed of three outlying specimens of *P. sumatrana*. This overlap has no doubt contributed to problems of classification and identification.

Sinclair (1955, p. 322) further indicated that *Polyalthia glauca* can be distinguished from *P. sumatrana* by its mature fruit "with thinner [carpel] stalks and pedicels." FIGURES 10 and 11 demonstrate that, again, while there are central tendencies in these species, the amount of overlap renders these characters of little use in discriminating clearly between the two species. In FIGURES 10 and 11 it can be seen that the length and width of carpel stalks and pedicels from mature fruits are not very useful in discriminating any of the species except perhaps the group comprising *P. hypoleuca* and *P. multinervis* Diels specimens. Even these are not clearly bounded from the *P. glauca* and *P. sumatrana* specimens.



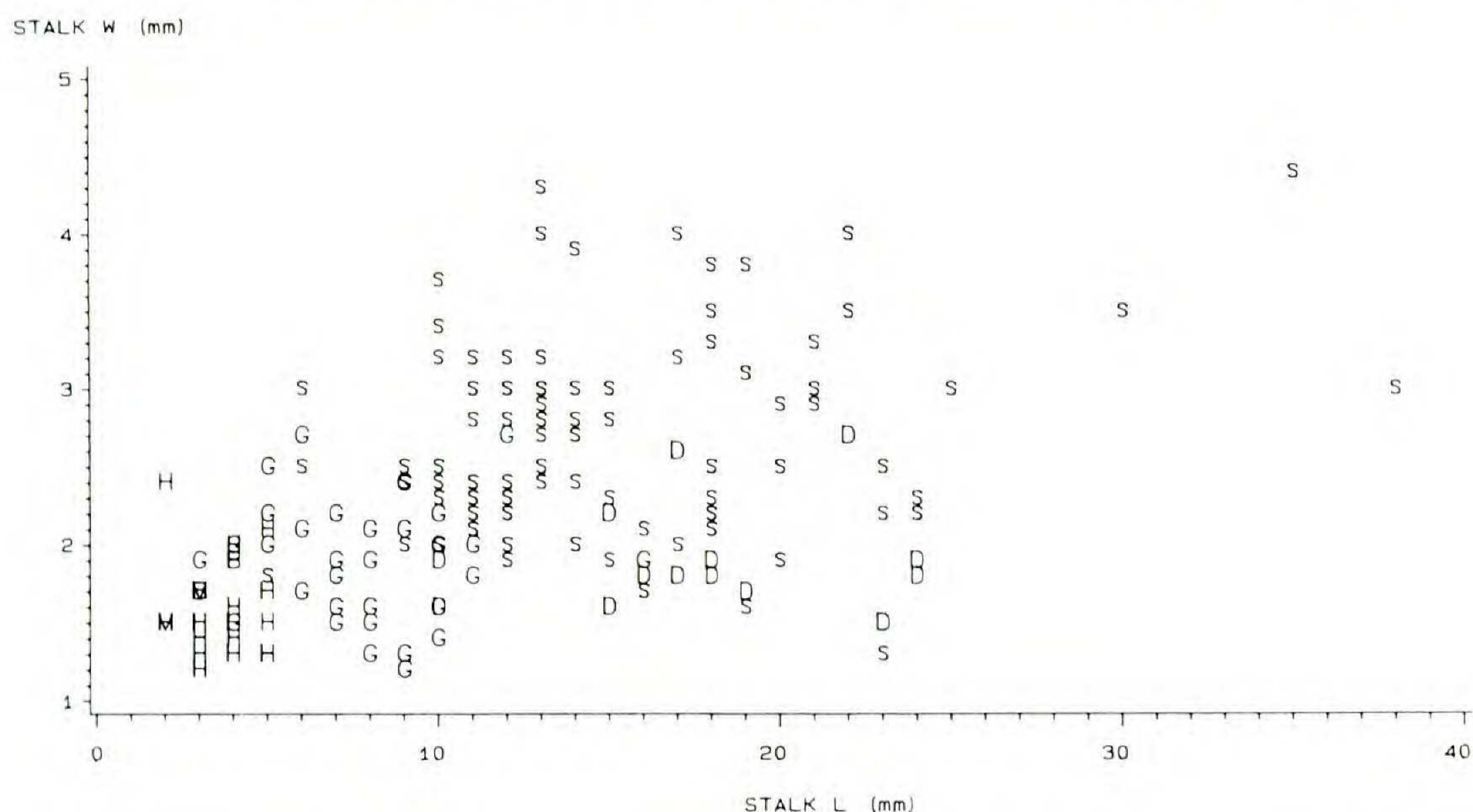


FIGURE 10. Stalk length vs. width for mature carpels of *P. hypoleuca* complex: B = *P. ovalifolia*, D = *P. discolor*, G = *P. glauca*, H = *P. hypoleuca*, M = *P. multinervis*, S = *P. sumatrana*.

An examination of floral characters used by Sinclair (1955) also suggests why herbarium workers have had problems identifying specimens in this group. For example, Sinclair described the petals of *Polyalthia glauca* as 16–20 mm long, and thus larger than those of *P. hypoleuca* (8–12 mm long). FIGURE 12 depicts the relationship of petal length to widest petal width for all the mature

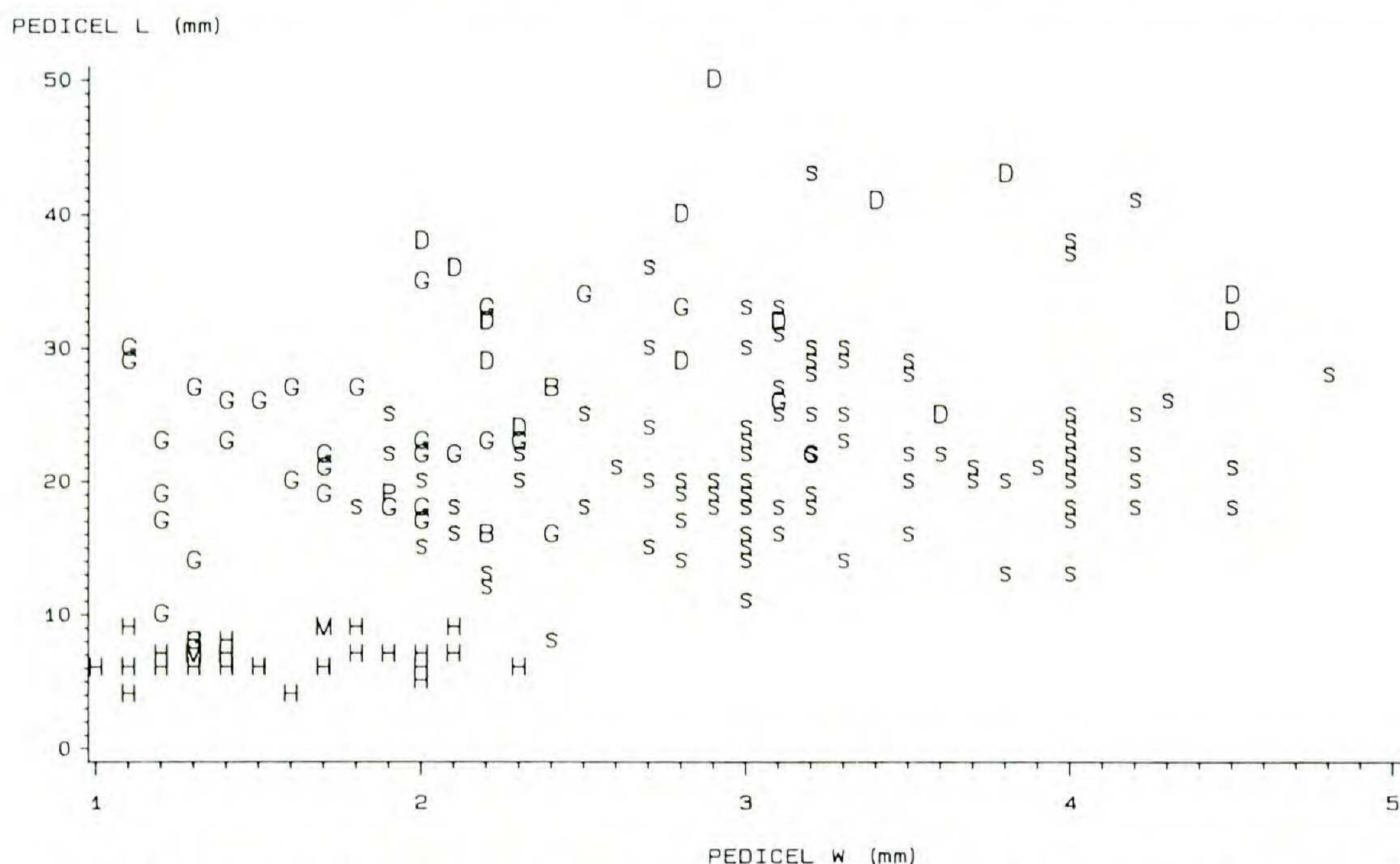


FIGURE 11. Pedicel width vs. length for mature carpels of *P. hypoleuca* complex: B = *P. ovalifolia*, D = *P. discolor*, G = *P. glauca*, H = *P. hypoleuca*, M = *P. multinervis*, S = *P. sumatrana*.



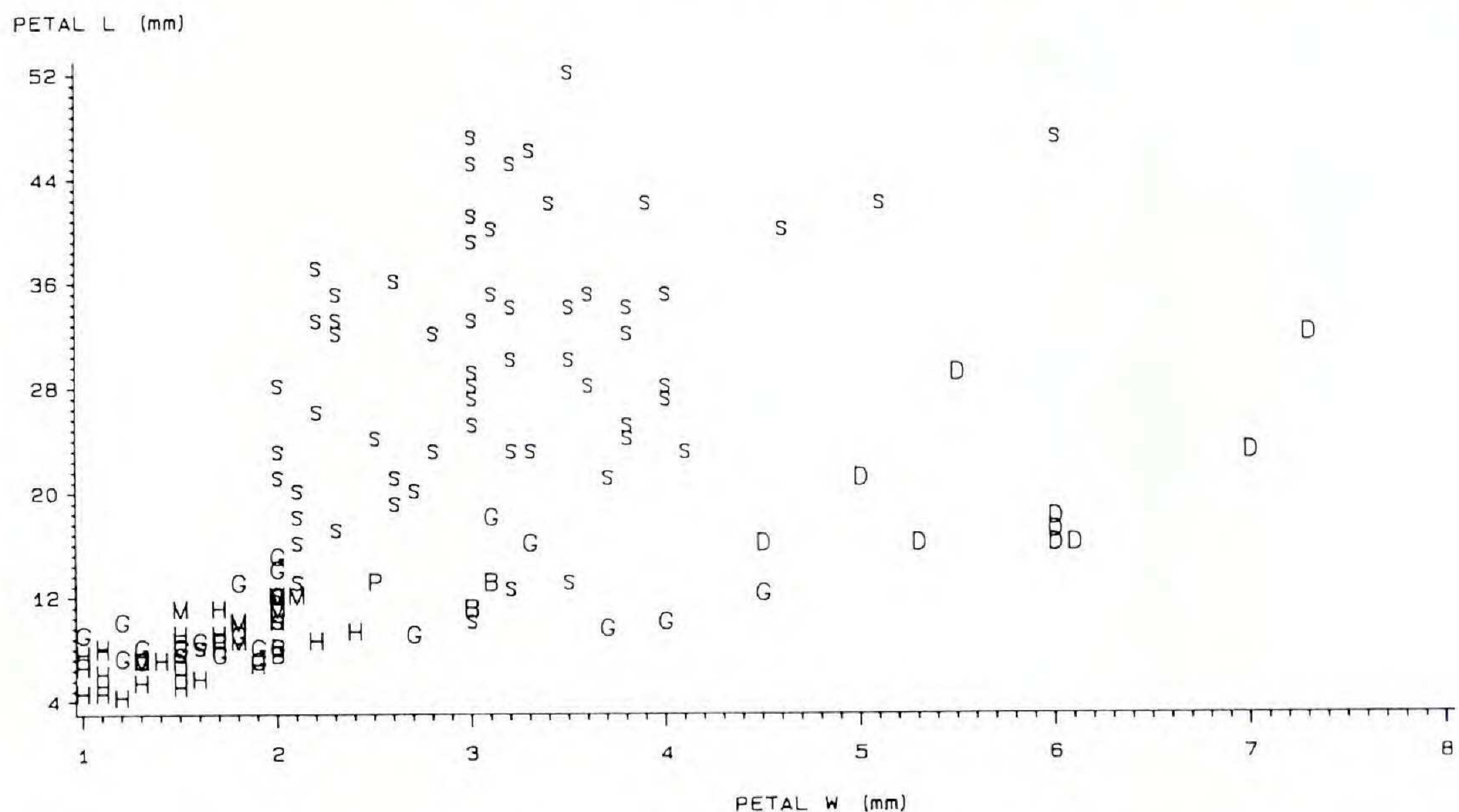


FIGURE 12. Outer petal length vs. width for mature flowers of *P. hypoleuca* complex: B = *P. ovalifolia*, D = *P. discolor*, G = *P. glauca*, H = *P. hypoleuca*, M = *P. multinervis*, S = *P. sumatrana*.

specimens of species that I have included in the *P. hypoleuca* complex, and again, with the possible exception of the *P. discolor* specimens, it is difficult, based on these characters alone, to demarcate any clear groups, let alone find support for Sinclair's proposed differentiation between the two species.

As noted earlier, hundreds of such character comparisons could be presented,

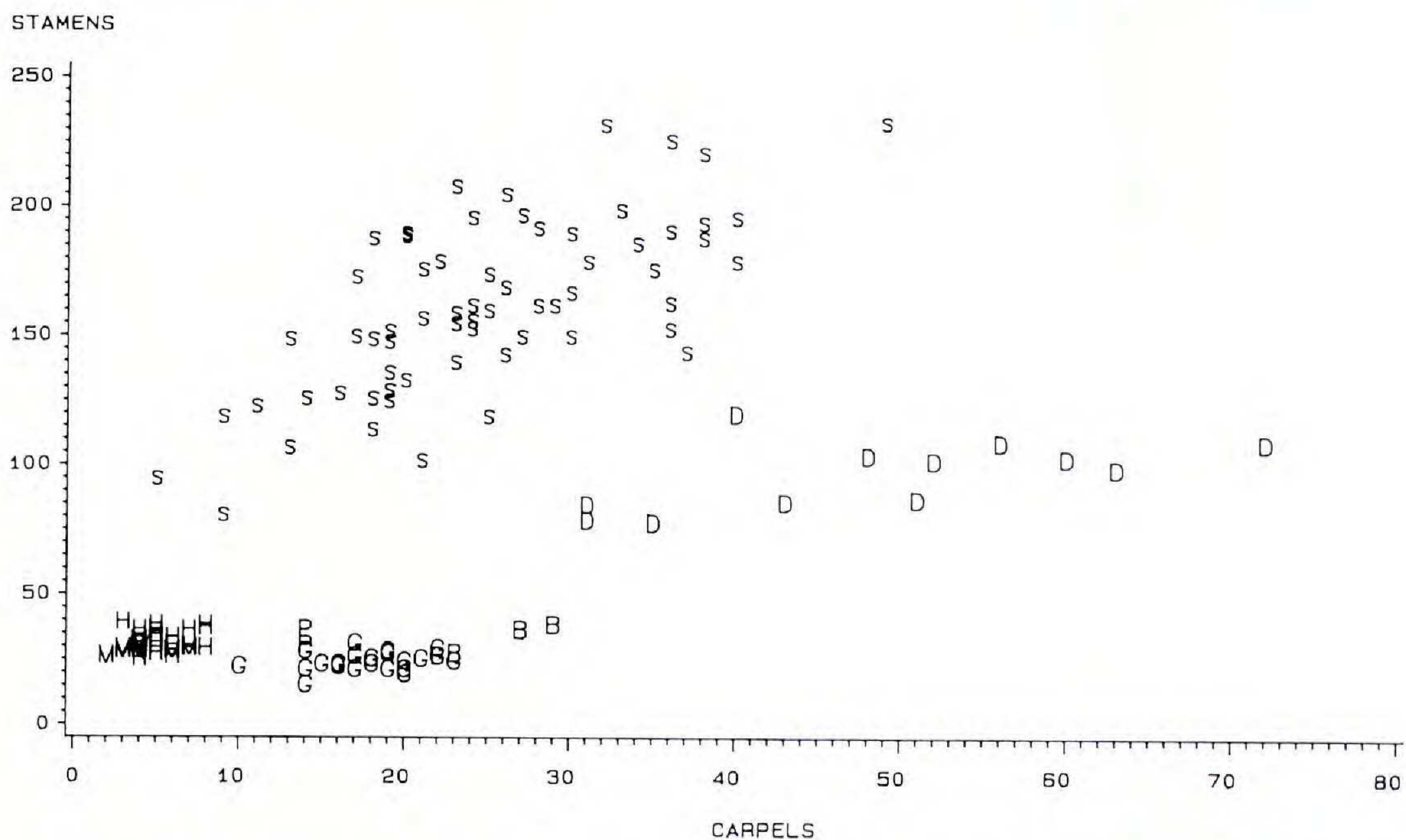


FIGURE 13. Stamen number vs. carpel number for mature flowers of *P. hypoleuca* complex: B = *P. ovalifolia*, D = *P. discolor*, G = *P. glauca*, H = *P. hypoleuca*, M = *P. multinervis*, P = *P. parkinsonii*, S = *P. sumatrana*.



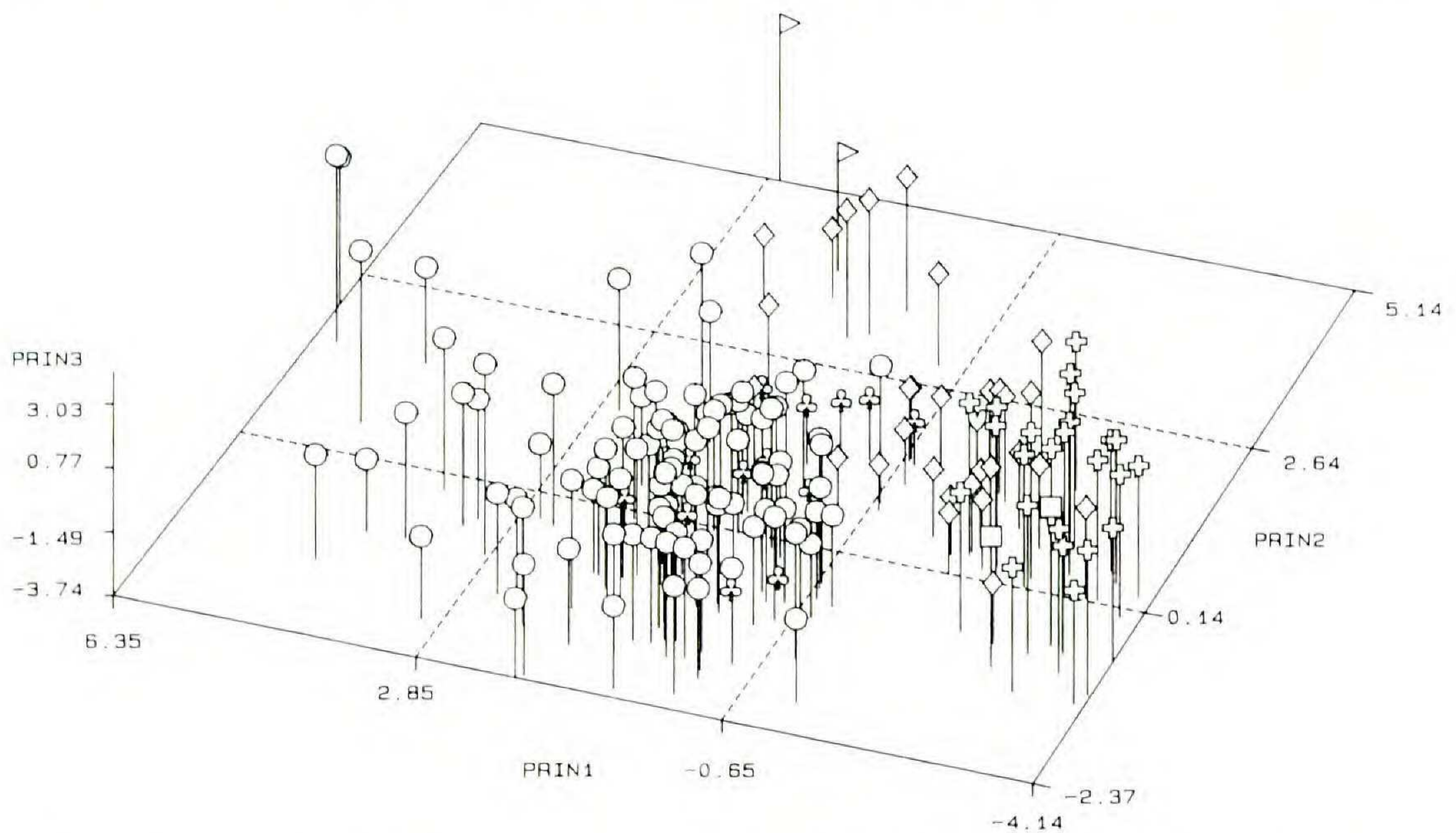


FIGURE 14. PCA results for continuous characters of mature fruits and leaves of *Polyalthia hypoleuca* complex. Each specimen depicted by its score on first 3 principal components ("PRIN") (details given in TABLE 1). *Polyalthia discolor* = clubs, *P. glauca* = diamonds, *P. hypoleuca* = crosses, *P. multinervis* = squares, *P. ovalifolia* = flags, *P. parkinsonii* = hearts, *P. sumatrana* = circles.

and all that I have inspected have shown the same pattern: when univariate or bivariate comparisons are made of mature vegetative, floral, or fruit characters, clear-cut groupings of specimens do not often emerge. In the herbarium the taxonomist examines not only mature specimens (as is the case in all the examples above) but also immature ones, often without any means of distinguishing between them. Obviously, this contributes even more to the uncertainty.

It could be argued that, just as in FIGURE 12 where the *Polyalthia discolor* group of specimens is more or less defined, if one looked at additional plots, other groups could be distinguished, and in this way a set of characters, each defining one taxon or more, could be found. With the present set of specimens, such clear patterns have rarely emerged from this data set, and in any case this procedure is perhaps of dubious general utility. It is more often the case that species show central tendencies with varying degrees of character overlap. As will be seen below, however, such overlap may often not be a problem in searching for groups if specimen data are examined with multivariate statistical techniques that analyze for patterns of characters that covary.

The relationship of stamen number to carpel number (see FIGURE 13) deserves special mention as it unexpectedly emerged as a powerful discriminator of most of the species. Here four rather well differentiated groups (*P. sumatrana*, *P. discolor*, *P. hypoleuca*–*P. multinervis*, and *P. ovalifolia*–*P. glauca*–*P. parkinsonii*) can be distinguished. Why these last two groups are composed of more than one species will be explained below. It is important to note that none of these groups is well defined by the number of stamens or carpels alone, but



TABLE 1. Loadings for first 5 components of continuous and meristic mature fruit and leaf characters\* derived from PCA of 195 specimens of *Polyalthia hypoleuca* complex.\*\*

CHARACTER	COMPONENT LOADINGS				
	1	2	3	4	5
Leaf L	0.847	0.375	0.130	0.026	0.035
Leaf W	0.744	0.475	0.134	0.187	-0.059
Mature carpel stalk L	0.715	-0.316	-0.288	0.032	0.279
Pedicel W at apex	0.713	-0.474	-0.094	0.128	0.180
Mature carpel L	0.699	-0.401	0.136	-0.263	-0.327
Mature carpel stalk W at apex	0.678	-0.432	0.049	-0.268	-0.234
Pedicel L	0.579	0.128	-0.610	0.112	0.329
Petiole L	0.524	0.492	0.109	0.367	-0.209
Leaf vein number	0.482	-0.134	0.645	0.193	0.019
Mature carpel W	0.317	0.435	-0.515	-0.468	-0.306
Leaf drip-tip L	0.178	0.343	0.472	-0.625	0.445

\*Listed in Appendix 3.  
\*\*The characters are listed in descending order according to loadings on the first component (L = length; W = width). The scores for each specimen with respect to the first three components are depicted in Figure 14. Of the total variance, the first five components accounted for 38.3, 14.7, 13.1, 9, and 6.5 percent, respectively.

rather the absolute numbers of stamens and carpels plus the quotient of the two must be considered in distinguishing these groups. These characters are not restricted in use to specimens bearing only intact flowers, since stamens and aborted carpels, after abscising, leave scars on the developing fruit. These characters have not generally been utilized by previous systematists working on this group; it is possible that they may also be important in distinguishing species of other species complexes in the Annonaceae.

Because clearly discernible groups were not apparent in the uni- and bivariate character examinations, multivariate statistical analyses were undertaken. Again, only a few of the most representative or meaningful trials will be discussed. All analyses yielded results similar to those selected as examples below. First, PCA was applied to search for possible groups based on suites of correlated characters, and once putative groups were determined, statistical testing of each specimen for membership in its assigned group was conducted utilizing a jack-knifed discriminant analysis.

FIGURE 14 presents the scores of each specimen with respect to the first three principle components resulting from the PCA of the continuous mature fruit and leaf characters. These components account for 66.1 percent of the total variance in the data set (TABLE 1 lists the component loadings of each character and the percent of the total variance explained by each of the first five components for this trial). Note that the only specimens in FIGURE 14 that have



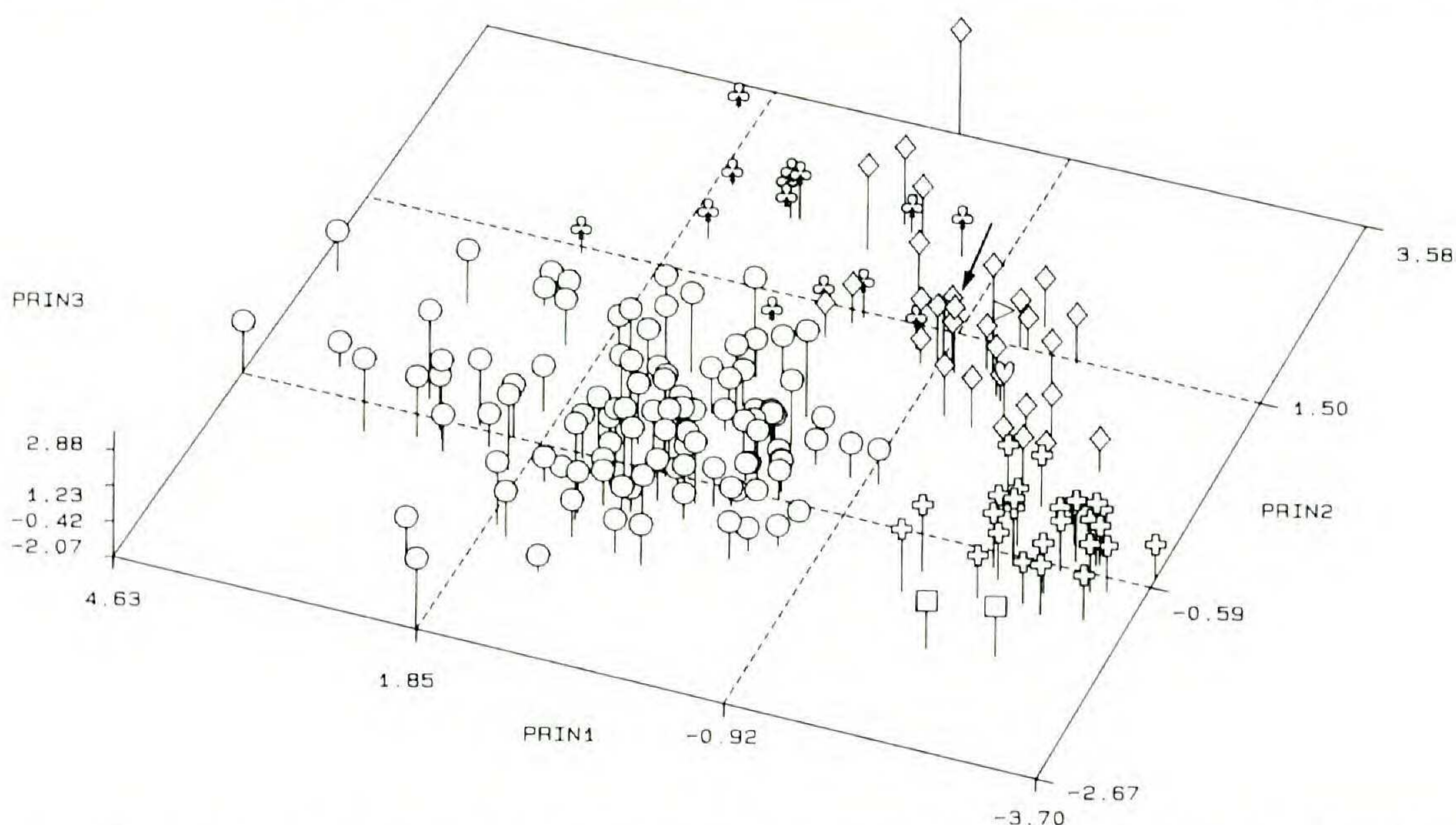


FIGURE 15. PCA results for continuous characters of mature fruits of *Polyalthia hypoleuca* complex. Each specimen depicted by its score on first 3 principal components ("PRIN") (details given in TABLE 2). Arrow points to obscured flag. *Polyalthia discolor* = clubs, *P. glauca* = diamonds, *P. hypoleuca* = crosses, *P. multinervis* = boxes, *P. ovalifolia* = flags, *P. parkinsonii* = hearts, *P. sumatrana* = circles.

densely pubescent pedicels and young shoots are the "flags" (*Polyalthia ovalifolia*) and the "crosses" (*P. hypoleuca*), which makes the "flag" specimens even more distinct.

Inspection of FIGURE 15, which is the PCA of the same data matrix used to generate FIGURE 14 but with the leaf characters removed, shows that fruit data alone yield a clearer grouping of the specimens; the first three components (see TABLE 2) now account for 83.9 percent of the total variance. For example, the *Polyalthia sumatrana* and the *P. hypoleuca* sets of specimens are now more distinct. Inclusion of the leaf characters with the continuous fruit characters, then, generally confounds the clearer clustering of specimens by the continuous fruit characters alone. It is interesting to note, however, that the *P. ovalifolia* specimens sit somewhat apart in the PCA of the fruit and leaf characters (FIGURE 14) but are placed with *P. glauca* when the fruit characters alone are analyzed (FIGURE 15). This difference becomes clear upon inspection of FIGURE 9, where the only two specimens of *P. ovalifolia* having all the fruit and leaf characters required for inclusion in the PCA analyses are set somewhat apart by leaf size.

If one considers some of the noncontinuous characters in conjunction with FIGURE 15, groups become more distinct. For example, only specimens here designated as *Polyalthia sumatrana*, *P. hypoleuca*, and *P. multinervis* have ellipsoid mature carpels; *P. glauca*, *P. discolor*, and *P. ovalifolia* have globose ones. Of these species, only *P. hypoleuca* and *P. ovalifolia* have densely pubescent pedicels in both flower and fruit, which further accentuates *P. hypoleuca* as a distinct group in FIGURE 15.

The partial lack of clear grouping by PCA of the continuous fruit characters alone helps explain the confusion that has existed among taxonomists who



TABLE 2. Loadings for first 5 components of continuous mature fruit characters\* derived from PCA of 195 specimens of *Polyalthia hypoleuca* complex.\*\*

CHARACTER	COMPONENT LOADINGS				
	1	2	3	4	5
Pedicel W at apex	0.822	−0.201	−0.264	0.365	0.164
Mature carpel stalk L	0.821	0.033	−0.307	−0.453	0.113
Mature carpel stalk W at apex	0.781	−0.302	0.301	−0.018	−0.449
Mature carpel L	0.768	−0.298	0.407	0.009	0.257
Pedicel L	0.609	0.609	−0.379	0.124	−0.165
Mature carpel W	0.297	0.779	0.513	0.012	0.090

\*Listed in Appendix 3.  
\*\*The characters are listed in descending order according to loadings on the first component (L = length; W = width). The scores for each specimen with respect to the first three components are depicted in Figure 15. Of the total variance, the first five components accounted for 50.1, 20, 13.8, 5.9, and 5.7 percent, respectively.

have attempted to classify fruiting specimens with globose mature carpels from New Guinea. Although Diels (1915) described the mature carpels of *Polyalthia discolor* as subglobose (the distal portion is in fact globose), every herbarium specimen from New Guinea with globose ones that I have encountered has been either identified as *P. glauca* or unidentified. This confusion is not difficult to understand since not only do both of these species have distally globose mature carpels, but as can be seen in FIGURE 15, they are not clearly separated by PCA of the continuous characters measured from mature fruit. Note, however, that there are central tendencies to the two groups that do result in some separation based on generalized size factors (see the heavily loaded characters in TABLE 2), since *P. discolor* fruits tend to be larger.

The problem of identifying these specimens has been solved by considering the floral data examined above. Recall that in FIGURE 13 *Polyalthia discolor* is well separated by stamen number from the group including *P. glauca*, *P. ovalifolia*, and *P. parkinsonii*. In most mature fruits of these two groups from New Guinea, the staminal portion of the torus retains scars of each stamen that it once bore, and these scars can be counted. Every specimen designated *P. discolor* in FIGURE 15 represents a collection with globose mature carpels and more than 60 stamen scars, while those specimens with globose mature carpels and less than 50 stamen scars were assigned to *P. glauca*.

No continuous, presence-absence, or subjectively coded characters were found to separate a specimen described by Hutchinson (1917)—and later recognized by Sinclair (1955)—as *Polyalthia parkinsonii* from the group of specimens assigned to *P. glauca*. Unfortunately, this entity has only been collected once



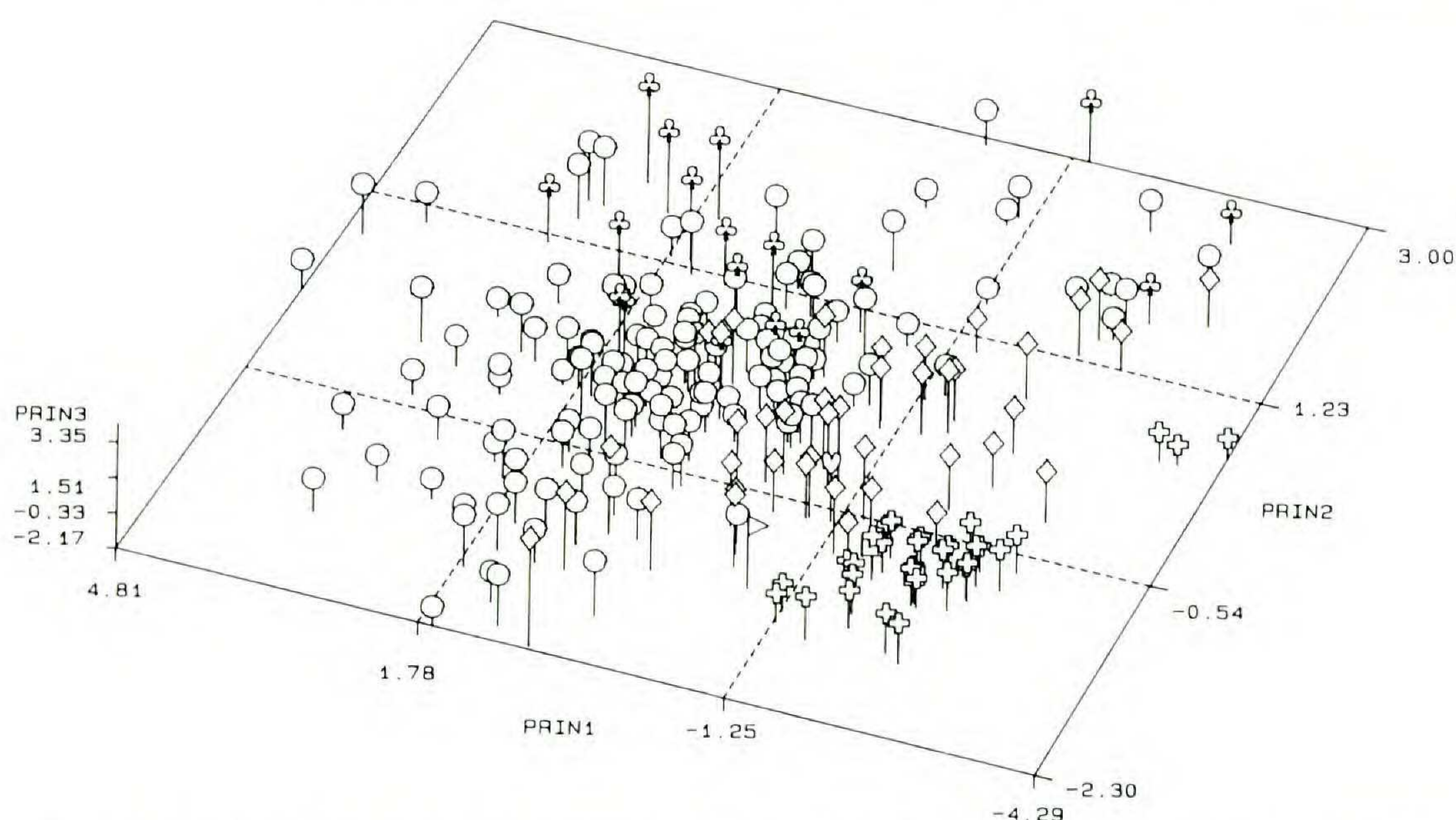


FIGURE 16. PCA results for continuous characters of mature plus immature fruits of *Polyalthia hypoleuca* complex. Each specimen depicted by its score on first 3 principal components ("PRIN") (details given in TABLE 3). *Polyalthia discolor* = clubs, *P. glauca* = diamonds, *P. hypoleuca* = crosses, *P. multinervis* = boxes, *P. ovalifolia* = flags, *P. parkinsonii* = hearts, *P. sumatrana* = circles.

in fruit, from the Andaman Islands, and no label data indicating the maturity of the fruit were available. Perhaps more extensive collection of this entity will demonstrate that it has mature fruit characters distinguishing it from *P. glauca*, but based on current data it cannot be separated.

Another major factor confusing the identity of herbarium specimens, and thus concepts of species in the *Polyalthia hypoleuca* complex, stems from specimens that are immature. The results depicted in FIGURE 16 were calculated by exactly the same PCA method utilized in FIGURE 15, except that data from immature fruit of most of the species have been added to the data set. TABLE 3 indicates that the first three components account for 85.5 percent of the total variance (and includes character loadings for this PCA). These immature fruits (noted as green on the herbarium labels, or obviously very much smaller than normal) have been identified to species by the presence of mature flower or fruit structures on the sheet or by some noncontinuous character specific to a species (e.g., dense pubescence on pedicel, as discussed above; red spots noted as present on green fruits (*P. sumatrana* only)). The inclusion of immature specimens in FIGURE 16 greatly disrupts the group structure recognizable in FIGURE 15. It is easy to understand from this example that using only continuous measurements of fruit characters emphasized by earlier workers may be misleading if immature specimens cannot be (or are not) distinguished from mature ones, a problem common with the Annonaceae.

The results of the multivariate analyses of the floral characters are similarly informative and also support changes of earlier concepts of species within this group. FIGURE 17 presents the scores with respect to the first three components



TABLE 3. Loadings for first 5 components of continuous mature and immature fruit characters\* derived from PCA of 234 specimens of *Polyalthia hypoleuca* complex.\*\*

CHARACTER	COMPONENT LOADINGS				
	1	2	3	4	5
Mature carpel L	0.824	0.430	0.099	0.028	0.082
Mature carpel stalk W at apex	0.817	0.214	0.311	0.081	-0.405
Mature carpel stalk L	0.802	-0.326	0.049	-0.493	0.055
Pedicel W at apex	0.785	-0.312	0.307	0.282	0.308
Mature carpel W	0.535	0.532	-0.617	-0.004	0.120
Pedicel L	0.515	-0.596	-0.555	0.168	-0.170

\*Listed in Appendix 3.  
\*\*The characters are listed in descending order according to loadings on the first component (L = length; W = width). The scores for each specimen with respect to the first three components are depicted in Figure 16. Of the total variance, the first five components accounted for 52.7, 17.9, 14.9, 6, and 5.2 percent, respectively.

resulting from PCA of the continuous floral characters of mature flowers. The character loadings for—and the percent of—the total variance explained by the first five components are given in TABLE 4, wherein 64.5 percent of the total variance is attributable to the first three components. As can be seen in FIGURE 17, the specimens assigned to the six species of the *Polyalthia hypoleuca* complex based on consideration of the total data analyzed are usually “clustered” in closer proximity to other conspecifics when plotted relative to only the first three components. Six rather distinct groups occur: *P. discolor*, *P. glauca*–*P. parkinsonii*, *P. hypoleuca*, *P. multinervis*, *P. sumatrana*, and (perhaps least distinct here) *P. ovalifolia*. As with the fruit data, no continuous, presence-absence, or subjectively coded characters could be found to distinguish the two specimens recognized by Hutchinson (1917) as *P. parkinsonii* from the specimens I recognize as *P. glauca*.

These groups are supported by considering the noncontinuous floral characters in conjunction with FIGURE 17. For example, the specimens designated as *Polyalthia ovalifolia* have very densely pubescent pedicels (both flower and fruit) and young shoots and can thus be distinguished from both *P. discolor* and *P. glauca*–*P. parkinsonii* specimens, which lack this pubescence (rare specimens are very sparsely pubescent). Also, as can be seen in FIGURE 9, specimens assigned to *P. ovalifolia* have larger, more widely elliptic leaves (the width/length quotient is statistically different for these specimens than for either *P. discolor* or *P. glauca* (see comments after the description of *P. ovalifolia*, below)) that set them apart from all of the other groups.

*Polyalthia ovalifolia* is poorly represented in the PCAs including characters of mature flowers (FIGURE 17) or fruits (FIGURE 15) because individuals with



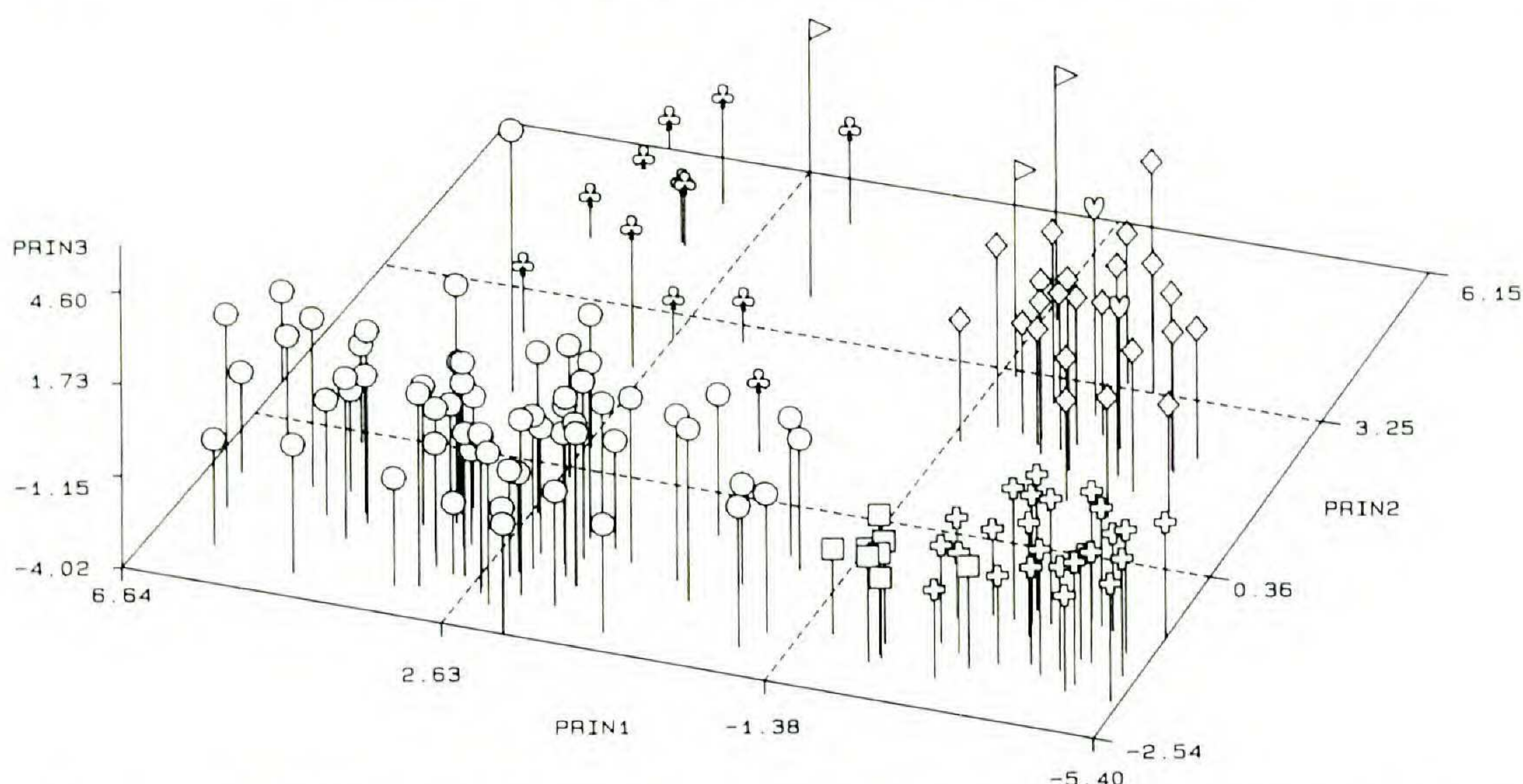


FIGURE 17. PCA results for continuous and meristic characters of mature flowers and leaves of *Polyalthia hypoleuca* complex. Each specimen depicted by its score on first 3 principal components ("PRIN") (details given in TABLE 4). *Polyalthia discolor* = clubs, *P. glauca* = diamonds, *P. hypoleuca* = crosses, *P. multinervis* = boxes, *P. ovalifolia* = flags, *P. parkinsonii* = hearts, *P. sumatrana* = circles.

mature flowers or fruits have rarely been collected. I have visited populations of this species (e.g., Bako Forest Reserve, Kuching, Sarawak; see MAP 1) but was unsuccessful in finding trees with mature flowers or fruits, although fragments of fruits (e.g., pedicels) were observed. Close to 40 individuals were found, and character states were recorded for several vegetative characters (some of these data are included in FIGURE 9). In these surveys and in all of the herbarium specimens I have examined, I have found no intermediates between the group designated as *P. ovalifolia* and the specimens I assign either to *P. glauca* or to *P. discolor*. Specimens of *P. ovalifolia* were previously either unidentified or annotated as *P. glauca*. For example, Sinclair (1955) included them in the latter species (e.g., see collection *S 12401*). However, based upon the distinctness of the sum of the vegetative and reproductive characters, I am recognizing this entity as a separate species, the formal details for which are presented below.

The group denoted as *Polyalthia multinervis* in FIGURE 17 also requires special mention since it can perhaps be argued that the groups I recognize as *P. hypoleuca*, *P. multinervis*, and *P. sumatrana* are not really distinct but in fact lie along a gradient of continuous character variation. Consideration of noncontinuous characters and field information in conjunction with this graph supports the conclusion that three distinct groups exist. First, all of the *P. multinervis* specimens are from Papua New Guinea, while all of the specimens comprising the *P. hypoleuca* and *P. sumatrana* groups are from Sulawesi or westward, so the variation pattern is not simply clinal. Also *P. multinervis* is very distinct from *P. sumatrana* in stamen and carpel numbers (see FIGURE 13), and from *P. hypoleuca* in having glabrous or very sparsely pubescent (vs. moderately to densely tomentose) pedicels on both mature flowers and fruits.



TABLE 4. Loadings for first 5 components of continuous and meristic mature flower and leaf characters\* derived from PCA of 135 specimens of *Polyalthia hypoleuca* complex.\*\*

CHARACTER	COMPONENT LOADINGS				
	1	2	3	4	5
Androecium W	0.942	-0.157	0.007	-0.120	0.051
Torus W	0.900	0.155	-0.009	-0.088	0.058
Pedicel W at apex	0.880	-0.213	-0.090	-0.035	0.002
Stamen number	0.874	-0.283	-0.113	-0.211	0.029
Inner petal L	0.854	-0.155	0.018	-0.232	0.078
Outer petal L	0.853	-0.150	-0.009	-0.238	0.138
Androecium H	0.834	-0.390	-0.023	-0.006	0.008
Pedicel W at base	0.822	-0.215	-0.084	0.022	0.001
Stamen L	0.771	-0.140	0.148	0.328	0.030
Gynoecium W	0.752	0.474	0.040	-0.084	0.091
Torus H	0.742	-0.319	0.001	-0.122	0.132
Carpel number	0.733	0.499	0.120	-0.145	0.067
Inner petal W	0.730	0.421	0.303	0.009	-0.081
Inner theca L	0.709	-0.234	0.104	0.353	-0.024
Outer petal W	0.688	0.478	0.300	-0.028	-0.087
Carpel L	0.678	-0.172	0.172	0.303	-0.088
Leaf L	0.525	0.363	-0.683	0.090	-0.060
Pedicel L	0.517	0.621	-0.011	-0.151	-0.207
Leaf vein number	0.457	-0.561	-0.280	0.167	-0.122
Leaf W	0.439	0.444	-0.669	0.090	0.071
Outer theca L	0.434	-0.079	0.248	0.738	-0.022
Stamen W	0.372	0.127	0.002	0.203	0.407
Peduncle L	0.349	0.254	0.421	-0.080	-0.456
Stigma L	-0.319	0.539	-0.081	0.287	0.122
Inflorescence flower number	-0.318	0.671	-0.004	0.006	0.110
Pedicel bract distance	0.284	0.621	0.096	-0.115	-0.341
Petiole L	0.227	0.604	-0.493	0.143	-0.027
Gynoecium emergence	-0.006	0.728	0.169	0.217	0.098
Leaf drip-tip L	0.005	-0.317	-0.374	0.131	-0.628

\*Listed in Appendix 3.  
\*\*The characters are listed in descending order according to loadings on the first component (H = height; L = length; W = width). The scores for each specimen with respect to the first three components are depicted in Figure 17. Of the total variance, the first five components accounted for 41.4, 16.4, 6.7, 4.8, and 3.7 percent, respectively.

Further, the flowers of *P. multinervis* are generally larger than those of *P. hypoleuca* (thus they cluster almost separately in FIGURE 17), and the mature carpels of *P. multinervis* are more acute at the apex than those of *P. hypoleuca*. Finally, the floral biology of members of *P. multinervis* is distinct from that of *P. hypoleuca*, as will be described in a subsequent article devoted to the comparative floral biology of the complex (Rogstad, in prep. b).



As with the analyses of the fruit data, inclusion of information from immature flowers in the data set used to generate FIGURE 17 (from mature flowers only) has a disruptive effect on the clustering of specimens seen there (results not shown).

The results of the PCA of the floral characters data, in combination with consideration of discontinuous characters and other information, support a hypothesis that the specimens of the *Polyalthia hypoleuca* complex aggregate in six groups. Therefore, a jackknifed discriminant analysis of the same data was undertaken to test the classification of each individual to its proposed group. Only one example of several possible permutations of characters or options chosen is discussed here. This particular example has been selected because it is representative of the general results obtained in all of the discriminant-analysis exploratory trials; it includes all the specimens for which all the characters could be recorded, so there is no bias due to characters that have been deleted prior to the analysis to "improve" the groups; and the procedure used (PROC BMDP DISC JACK) is here computed to reflect the unequal sample sizes (PRIORS).

In this analysis the first three discriminant functions accounted for 96.2 percent of the total dispersion, and the weighting of the coefficients for the (canonical) variables for these functions reflects the pattern found in the PCA analyses described above. Over all the discriminant functions, each species as designated *a priori* from the results of these PCA trials has a class mean that is significantly different (F test;  $p < 0.01$  in all comparisons) from those of the other species. All of the specimens assigned to *Polyalthia glauca*, *P. discolor*, and *P. ovalifolia* from the PCA results were classified similarly in the jackknifed discriminant analysis, while 98.4 percent of the *P. sumatrana* specimens were placed in the latter analysis in accordance with the former (one of the 61 specimens of *P. sumatrana* was placed into *P. multinervis*).

As noted above, *Polyalthia hypoleuca* and *P. multinervis* are very similar to one another with respect to their continuous characters, although *P. multinervis* has slightly larger flowers. These similarities are reflected in the fact that, while the class means of these two species are statistically different, one of the 25 *P. hypoleuca* specimens and one of the eight *P. multinervis* specimens (both as determined by PCA of this data) were placed in the alternate class in the jackknifed discriminant analysis. However, differences in noncontinuous features separate these species (see above), and my decision to recognize them as distinct is founded on the totality of this evidence.

Finally, it should be noted that significant differences exist among these species with regard to vegetative and floral characteristics that could not be included in the above morphometric investigations, and these differences will be discussed in the species descriptions.

#### SUMMARY AND DISCUSSION

This investigation began with the grouping of a number of specimens possessing a suite of seven characters that distinguishes them from the rest of the Annonaceae.



However, some of the character states found within this monophyletic group conflict with previous attempts at classifying it within the genus *Polyalthia* and even with tribal placement. This conflict demonstrates that just because two species have been recognized as congeneric does not permit the conclusion that they are mutual members of a small monophyletic group, or that the species are "closely related" (see Heywood & Fleming (1986) for an example of TLRF sympatric congeners that are apparently only distantly related). For reasons noted earlier the establishment of monophyletic relationships is essential *before* attempting to utilize such congeners to examine the significance of whether or not sympatric closely related species differ in their niche characteristics.

Univariate, bivariate, and multivariate analyses (including PCA followed by confirmatory discriminant analysis) of morphological data recorded from specimens included in the *Polyalthia hypoleuca* complex determined that, while many of the characters previously used to distinguish these species showed central tendencies, enough overlap existed to cause confusion. In fact, subjective weighting of characters that overlap two or more species appears to have been an important source of previous species identification error.

Further, although PCA of a data set including only the continuous fruit characters revealed the similarity in PCA space of some of the specimens, noncontinuous characters are ultimately crucial in identifying fruiting specimens of this group. Exploration via PCA of covariance patterns of continuous and meristic floral and leaf characters among specimens, complemented with an analysis of the distribution of noncontinuous characters and other information, revealed groups of greater clarity. The statistical significance of these groups was tested and demonstrated through jackknifed discriminant analysis of the same data set. Ultimately, then, these analyses have provided a means to evaluate the characters previously used to define entities in this group, resulting in the rejection of some of these characters, the discovery of new ones, and thus a modification of concepts of the taxa within the *Polyalthia hypoleuca* complex. These characters have been used in constructing the keys to and descriptions of the species presented below.

Perhaps the subjective consideration of large numbers of specimens and characters, and the occasional overlap of character states between otherwise well defined species, partially accounts for the fact that of the 484 specimens examined and identified in accordance with these analyses, 9.7 percent had original identifications and 8.5 percent had subsequent annotations that differed from those presented here. Obviously, the possibility exists that the previous classification protocols and identifications are more correct. However, the analyses presented here utilize explicitly stated and repeatable techniques and character data that future workers can add to or manipulate to examine my conclusions.

The results of the morphometric analyses contribute to the rejection of the first of the three competing hypotheses, specifically that the *Polyalthia hypoleuca* complex is better described as a single polymorphic species. Further, the results support the conclusions that the complex comprises six morphologically distinct entities, and that these distinctions hold over very large geographic areas (see MAPS 2–5; more detailed ones are given in Rogstad, 1986). In other



words, no matter what reticulate and clinal variation patterns exist within these species, there are clear morphological discontinuities among them. In subsequent, related articles (Rogstad, in prep. a, b) further evidence will be presented that contributes to the rejection of Hypothesis I and bears on the choice of one of the two remaining hypotheses as the more applicable with regard to the *P. hypoleuca* complex.

One group of specimens that requires further discussion has been designated as *Polyalthia parkinsonii* in the results presented above (see FIGURES 15 and 17, "heart" symbol). As discussed earlier, Hutchinson (1917) and Sinclair (1955) recognized these collections from the Andaman Islands as a separate species. Unfortunately, only three collections with flowers or fruits have been made. With the material available I have been unable to find a single character, much less a suite of them, by which these specimens can be distinguished from those of *P. glauca*. I have therefore recognized *P. parkinsonii* as a synonym of *P. glauca*. Further collections and ecological observations of the Andaman entity may prove these conclusions incorrect.

I did not expect to find that *Polyalthia glauca*, the most widely distributed species of the *P. hypoleuca* complex, shows relatively little variation in comparison to the more-restricted *P. sumatrana* or *P. discolor* (see FIGURES 15, 17; MAPS 2–4). This apparent morphological uniformity in *P. glauca* may be a sampling error, but if it holds as the species becomes better collected, it must be explained in terms of genetic, developmental, and/or selective factors.

In contrast, *Polyalthia sumatrana* shows the greatest range of morphological variation, a finding that I believe to be true based on field examinations of this species (and see the comments under *P. sumatrana*, below). Part of this variation could well be correlated with smaller-scale, intraspecific geographic distribution patterns, a possibility that is currently being explored by a more detailed analysis of the data.

Note that large ecological differences have been found between very similar species, as with the differences in floral biology between *Polyalthia hypoleuca* and *P. multinervis* (Rogstad, in prep. b), and possibly even within what appear here to be morphological species. Thus, individuals of *P. glauca* were found on hilltops in southern Thailand but were restricted to poorly drained sites at Pasoh Forest Reserve, Malaysia. There are also flower-color morphs in *P. sumatrana* (see description of this species below). Such examples serve as a reminder that differentiation of cryptic or sibling species, which are difficult or impossible to distinguish on morphological characters, may be an important constituent of TLRD diversity and evolutionary processes.

The morphological analyses and resultant systematic treatment presented in this study form the foundation for investigations into the comparative autecologies of the designated species of the *Polyalthia hypoleuca* complex. Obviously, a clear concept of species is an absolute prerequisite for the study of sympatric, closely related or very similar entities in the field. While no hypothesis of the phylogeny of the *P. hypoleuca* complex is presented here, analyses using data gathered for this treatment are in progress to provide one. The resultant hypothesis, combined with information concerning the ecological



divergence of the species in the complex (Rogstad, in prep. a, b), will be examined in a future article to shed light on the evolution of geographic distribution and niche divergence among the members of this small monophyletic group.

#### THE POLYALTHIA HYPOLEUCA COMPLEX

##### General Description

The genus *Polyalthia* Blume (Fl. Javae, 68. 1830) is usually included in tribe Unoneae since the members have two series of petals that are valvate in bud and at maturity are similar or subsimilar and free (but see below). Within the Unoneae, the genus is distinguished by a combination of characters: members are trees or shrubs, with the petals not strongly clawed or basally attenuate, the stamen connectives flat topped or convex, the stigmas globose, rectangular, or irregularly shaped, the mature carpels thin walled (hardly greater than 1 mm) when dry, and the seeds one to five. Three sections have been recognized: sect. *Polyalthia* (formerly *Eu-Polyalthia* Blume), with bisexual flowers and two or more ovules per immature carpel; sect. *Monoon* Miq., with bisexual flowers and only one ovule per immature carpel; and sect. *Afropolyalthia* Engler & Diels, the members being andromonoecious, with compressed stamen connectives and connivent petals (the last section is in dispute; e.g., see Le Thomas, 1969; Verdcourt, 1969).

The *Polyalthia hypoleuca* complex of sect. *Monoon* can be diagnosed as follows: bark white, often mixed with shades of yellow or red on older twigs and branches; leaves with undersides having short, very dense, uniformly distributed papillae, the secondary veins very fine and almost indistinguishable from the tertiary veins, closely spaced and thus dense; pollen monosulcate, boat shaped, the tectum psilate, with medium-sized perforations, the pollen wall with regular columellae and a bipartite foliated basal layer; endosperm with ruminations needlelike. Another potentially useful character is the presence of straight, thickened anticlinal walls in all (or most) cells of the adaxial leaf epidermis.

Although the correct placement of this complex may not be in the genus *Polyalthia*, much more information regarding the possibly related taxa is needed before a clearer determination of the phylogenetic relationships of this group can be made. Until then, I have chosen the conservative option of retaining the complex within *Polyalthia*. I refer to this assemblage as the *P. hypoleuca* complex since *P. hypoleuca* was the first species of this group to be assigned to the genus.

##### Growth Characteristics

The six species of the *Polyalthia hypoleuca* complex share certain additional characteristics that may be helpful in distinguishing them, either in the field or as herbarium specimens, from other species of the genus. The seedlings are cryptocotylar, the cotyledons not emerging from the seed coats. This distin-



guishes them from *P. jenkinsii* (Hooker f. & Thomson) Hooker f. & Thomson and *P. rumphii* (Blume) Merr., and perhaps from other species allied with these two, which are phanerocotylar, the cotyledons expanding and remaining green while several true leaves develop after the seed coats have been shed. In the *P. hypoleuca* complex the hypocotyl elongates and becomes erect, bearing the cotyledons and epicotyl still enclosed in the cotyledons, while in *P. lateriflora*, *P. longifolia*, and *P. sclerophylla* (and perhaps other species allied with them) the hypocotyl does not elongate substantially, and the cotyledons, enclosed in the seed coats, remain at ground level. Above-ground shoot growth in these three species begins with elongation of the basal epicotyledonary internode. In members of the *P. hypoleuca* complex, a few weeks after the hypocotyl has become erect, the epicotyl and the first leaf primordia expand, gradually forcing the seed coats (still bearing the now-abscised cotyledons) to be shed.

The pattern by which seedlings of the *Polyalthia hypoleuca* complex grow (once branching from the axillary buds of leaves of the orthotropic shoot has commenced) appears to be common to seedlings (and saplings and trees) of most or all members of the genus. (The patterns of growth of trees of some Annonaceae—some *Xylopia* species, for example—are somewhat different; Rogstad, unpubl. data.) This pattern most closely agrees—at least for older seedlings—with Roux's model (Hallé *et al.*, 1978). To understand it, one must first realize that the primary phyllotaxy in most or all Annonaceae is distichous. In seedlings of *Polyalthia*, the second true leaf is borne 180° alternate to the first when fully expanded. The mature third leaf is, however, not oriented 180° from the attachment of the second one, but at an angle approximately 50–70° greater or less than this, and so it is not directly above the first leaf. Since these leaves are borne on an orthotropic shoot, such a pattern reduces the shading of the first leaf by the third.

This displacement of the third leaf from its expected position is effected by a "rotation" (presumably caused by differential growth) of the internode immediately below it as that internode and the third leaf expand. As in many Annonaceae, the terminal bud is held nearly horizontally due to the curvature of the internode above the last fully expanded leaf. The rotation of this curved internode occurs simultaneously with its straightening and elongation, and with the growth of the leaf immediately above it. The fourth leaf is usually borne on the orthotropic shoot at an angle of 180° to the third one, but as the third leaf is rotated away from its expected position over the first, so the fourth one is rotated away from its originally expected position over the second. The fifth leaf is again rotated from its expected distichous position relative to the fourth.

This rotation of every odd-numbered leaf (beginning with the third) is the usual initial growth pattern for the species of the *Polyalthia hypoleuca* complex (and for several other species in both this genus and various others). The rotation can be either clockwise or counterclockwise, and the direction appears to be constant in each seedling. It is also often the case in the *P. hypoleuca* complex, and possibly for other taxa as well, that the second true leaf is rotated relative to the first, with the third borne distichous to the second, the pattern described above continuing but offset by one leaf—that is, even-numbered leaves rotating (FIGURE 7A). In young seedlings, and especially in older ortho-



tropic shoots, rotation away from distichy may occasionally occur more frequently, that is, from leaf to leaf. This rotation of leaves continues in vertical shoot growth throughout the life of a tree. It has been observed as the pattern of terminal-bud expansion even in the uppermost shoots of newly fallen 20–34 m mature trees of *P. glauca* and *P. multinervis*.

Whether each leaf or every third leaf is rotated, the result is a more or less spiral leaf arrangement on vertical shoots. Although it appears from a simple inspection of the leaves on vertical shoots as though primary phyllotaxis is other than distichous, this is a secondary phenomenon. Note that as leaves are rotated away from primary distichous orientation, so are their axillary buds and the branches that develop from them—thus the spiral arrangement of the branches of many trees in the Annonaceae.

Another aspect of this growth pattern is not only characteristic for the members of the *Polyalthia hypoleuca* complex but also appears to be widespread in the family. After the third to eighth leaf of the vertical shoot of a seedling expands, further development of the terminal bud is suspended. During this period of suspension, an axillary bud of the latest expanded leaf will grow, forming a plagiotropic branch with fully expanded leaves. Primary distichous phyllotaxy persists on such branches, and the petioles of their leaves twist so that, when fully expanded, the laminae are more or less horizontal. Once such a lateral, plagiotropic branch bears five or more expanded leaves, the basal leaf and the internode immediately below it of the resting terminal bud resume growth. When they have achieved full size, the terminal bud rests again while the axillary bud of the newly expanded leaf is released, generating a new plagiotropic branch.

This rhythmic cycle of vertical-shoot growth, suspension of vertical-shoot growth, and plagiotropic-branch growth, followed by vertical-shoot growth, and so on, is one of the basic growth patterns in the Annonaceae and is common to all members of the *Polyalthia hypoleuca* complex. Above, I noted that this pattern is most consistent with Roux's model for *older* seedlings. This distinction was made because in younger seedlings (up to the stage where three to eight leaves are present on the orthotropic axis), axillary buds usually fail to develop into branches (see FIGURE 7A). In younger seedlings where only one or a few axillary branches have been initiated, the axillary bud of one or more leaves on the orthotropic shoot sometimes fails to develop into a branch, with such branches growing only from higher leaves. This irregular branching pattern, resembling Massart's model (Hallé *et al.*, 1978), is not usually found on older seedlings and saplings where lateral branches develop from the bud of every leaf of the orthotropic shoot (Roux's model). Interestingly, a return to Massart's model often accompanies the early growth of an axillary bud that assumes orthotropic shoot growth after the abortion of the true apical meristem and terminal bud of an orthotropic shoot. This axillary bud usually develops from the axil of the last fully expanded leaf on the orthotropic shoot and may generate two to five fully expanded leaves on the shoot, all with their axillary buds repressed, before a lateral branch is generated from the axil of the next leaf of the shoot to expand, thus resembling Massart's model.

In vertical growth the trees are monopodial, with one axis remaining the



“dominant” shoot unless its apical meristem dies, in which case another recently generated shoot takes its place. A few mature individuals of *Polyalthia glauca* have been found that have two major axes. As noted above, the lateral branches are initiated with a strong horizontal orientation, and lower branches are horizontal or initially “swoop” downward before bending upward to a nearly horizontal disposition distally.

### General Characteristics

All members of the *Polyalthia hypoleuca* complex are understory to main canopy trees, and although none of them develops large buttresses, boles of larger trees are often slightly fluted. In some species there are pronounced “hoop marks” from branch scars on the lower main bole, while in others such scars are not readily apparent. Although *P. glauca* is unique in this group in developing undulating pneumatophores, none of these species develops extensive stilt roots originating well above the soil surface, as do some Annonaceae (e.g., *Xylopia* spp.).

As noted above, at the very earliest stages of bark development, all the members of the *Polyalthia hypoleuca* complex have a generally smooth, pale white to yellowish white bark; this is mixed with pale reddish spots in some of the species. The greatest departure from this condition occurs in *P. discolor* and *P. glauca*, in which the bark on upper portions of the bole becomes papery and flaking (FIGURE 6C), white in the outermost layer and red underneath. Bark characteristics are usually retained throughout the life of the trees (see FIGURE 6A–C); they can readily be seen on herbarium specimens and provide a useful means of finding and identifying species of this complex in the field. They also distinguish the members of this group from all other species complexes of the genus, including those from Africa and Madagascar, as well as from most other Annonaceae (e.g., see Sinclair, 1955).

The distinctive leaf papillae and venation characteristics (see FIGURES 3 and 4) shared by all members of the complex have been described. Leaf shape, except in *Polyalthia ovalifolia* (elliptic to widely elliptic), is narrowly elliptic, with apices acute to caudate in all species (see FIGURE 3A). The adaxial leaf surfaces (including the sunken midvein) are glabrous and are tan to brown (occasionally olive or gray) when dry. The venation is even less distinguishable adaxially than abaxially. The margins are recurved. All species of this group are evergreen, and most, if not all, are capable of producing two flushes of new leaves a year (Rogstad, in prep. b).

The inflorescences of the *Polyalthia hypoleuca* complex develop in the axils of either present or abscised leaves. In all but one species, I have interpreted the inflorescences as comprising a very short peduncle (usually not longer than 2 mm, and lacking lateral buds and developing flowers) that terminates distally in an articulation subtended by a bract, beyond which an unarticulated pedicel develops. The exception, *P. discolor*, has elongate (up to 11 mm) peduncles that clearly have lateral buds and developing flowers. As in many of the Annonaceae, the members of the *P. hypoleuca* complex often generate serial buds; these give rise to several inflorescences per leaf axil, each with its own peduncle.



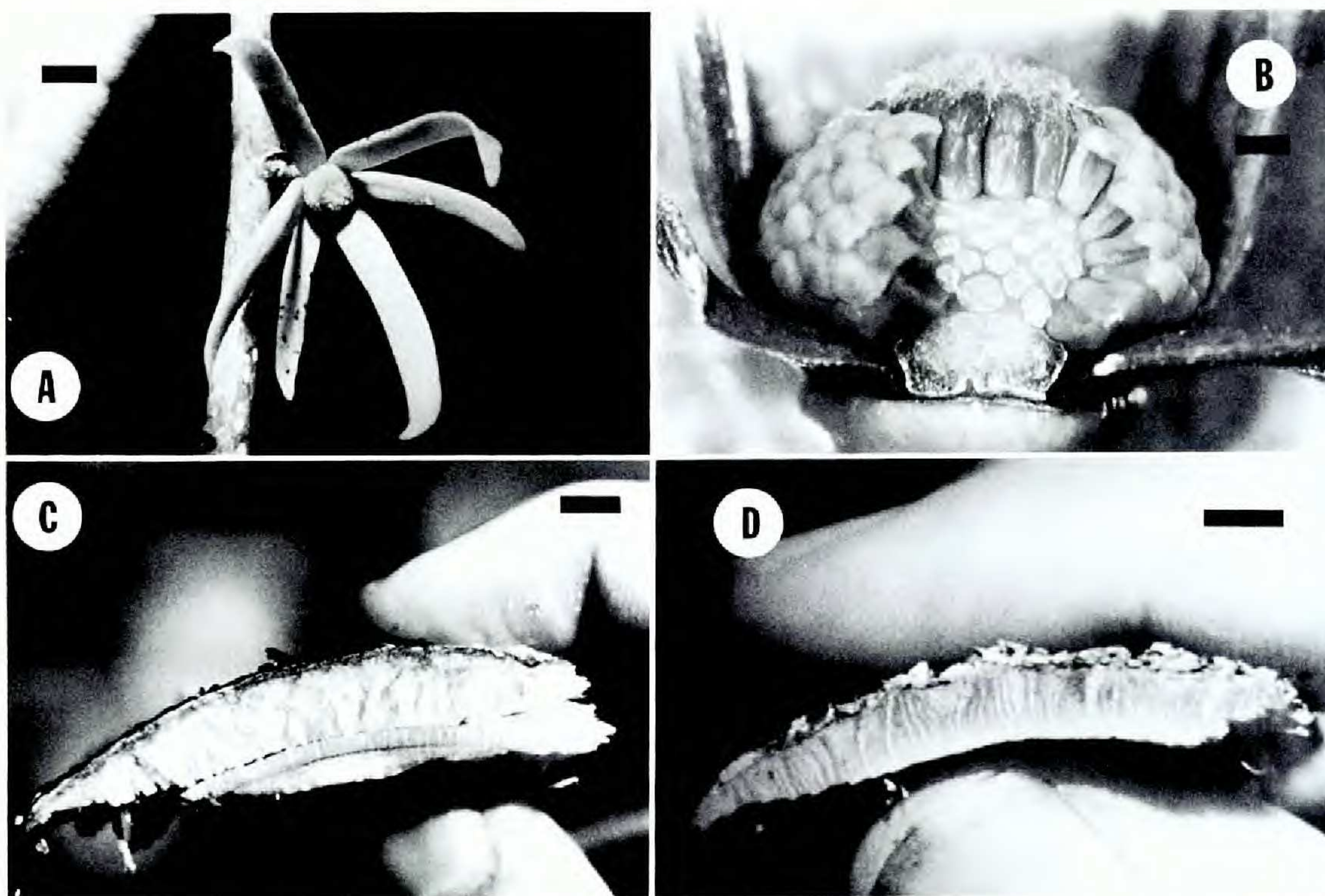


FIGURE 18. A, B, *Polyalthia sumatrana* (Rogstad 508), nearly mature flowers; scale bars = 5 mm in A, 0.5 mm in B. C, D, extremes of slash characteristics of mature trees in *P. hypoleuca* complex: C, *P. glauca*, relatively dispersed phloem rays not regularly reaching to epidermis, scale bar = 3 mm; D, *P. hypoleuca*, relatively dense phloem fiber rays regularly extending to epidermis, scale bar = 5 mm.

In species with few serial buds per axil (*P. hypoleuca*, *P. multinervis*, and *P. sumatrana*), usually no more than five inflorescences, and hence flowers, are found at any one axil (FIGURES 18A; 19A, C), and perennial tubercles built up from the remnant structures of previous flowering rarely develop at points of flowering. At axils where these species bear only one flower, peduncle bracts are perpendicular to the branch axis. In contrast, *P. discolor*, *P. glauca*, and *P. ovalifolia* all develop massive, perennial, ramiflorous tubercles, often with numerous flowers (more than ten; see FIGURE 20A, C). These tubercles are built up from the remnants of old inflorescences in the axils of abscised leaves. The bracts of the peduncles arising from these tubercles may be oriented in any direction.

Fries (1959) has argued that the presence and nature of pedicel bracts require more investigation as possible indicators of phylogenetic relationships, but in the species of the *Polyalthia hypoleuca* complex, they are very variable even within species. The pedicels are burgundy to blackish red when dry, and their pubescence is a key character for species identification.

The sepals of this group usually resemble equilateral to slightly extended or shortened isosceles triangles with glabrous adaxial and slightly to densely tomentose abaxial surfaces. They are more often caducous in some species (e.g., *Polyalthia hypoleuca*) than in others.

The petals of the two series are approximately equal in size and are always



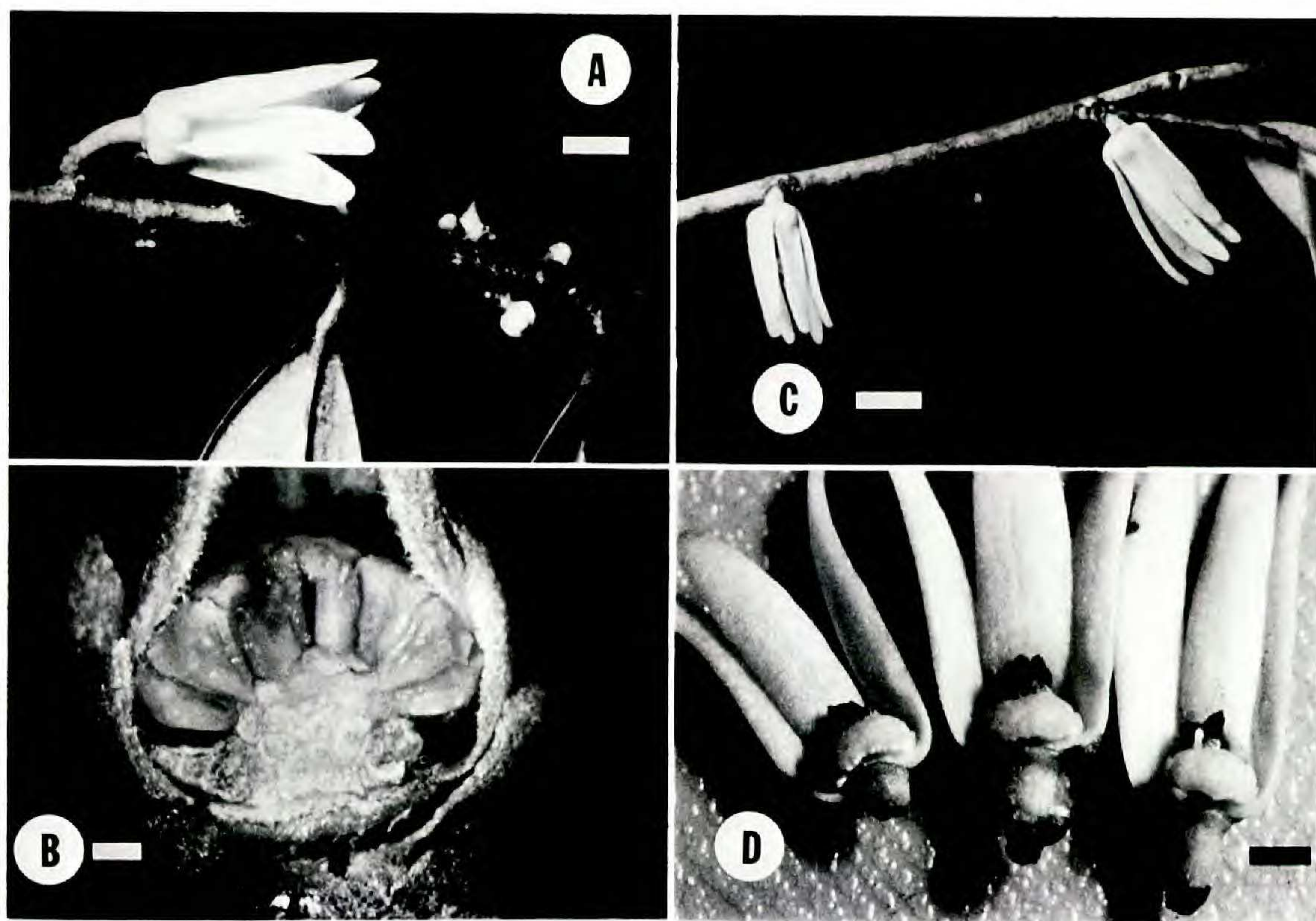


FIGURE 19. Flowers: A, *Polyalthia multinervis* (Rogstad 813), at anthesis, scale bar = 1 cm; B, *P. multinervis* (Rogstad 813), immature, scale bar = 0.5 mm; C, D, *P. hypoleuca* (Rogstad 912), just prior to anther dehiscence (note blackened stigmas in D), scale bars = 1 cm in C, 5 mm in D.

free throughout development. Green in all species until the stigmas become receptive (i.e., glistening with an exudate), they then turn various colors and may become fragrant. Occasional trees of all species of the complex sporadically have a few flowers with seven or eight petals, with two or more that are fused, or with one or more that fail to develop fully. The petals are linear to narrowly elliptic, and in some species they are occasionally flared distally and/or have a slight constriction near the base. Petals in which this constriction is pronounced are referred to as "clawed." The basal adaxial quarter is concave, glabrous, and often somewhat corrugated. The petals are otherwise flat; they are thin throughout, rather than thick and fleshy as in some Annonaceae.

The stamens are normal for the genus, with flat-topped to slightly convex connectives. On the torus each stamen is surrounded by a slightly raised ridge, which remains after the stamen has abscised and often even persists in the mature fruit. The resultant "stamen scars" can usually be counted and are therefore often crucial in species determination (see the discussion about the difficulty of identifying fruiting specimens of *Polyalthia glauca* and *P. discolor* from New Guinea, below). The portion of the torus bearing the stamens is short-columnar, forming a cylinder parallel to the floral axis, while that bearing the carpels may be concave, flat, or convex, varying even within a species (e.g., *P. sumatrana*). Both the androecial and the gynoecial portions of the torus are glabrous in all members of this group. This contrasts with several other species



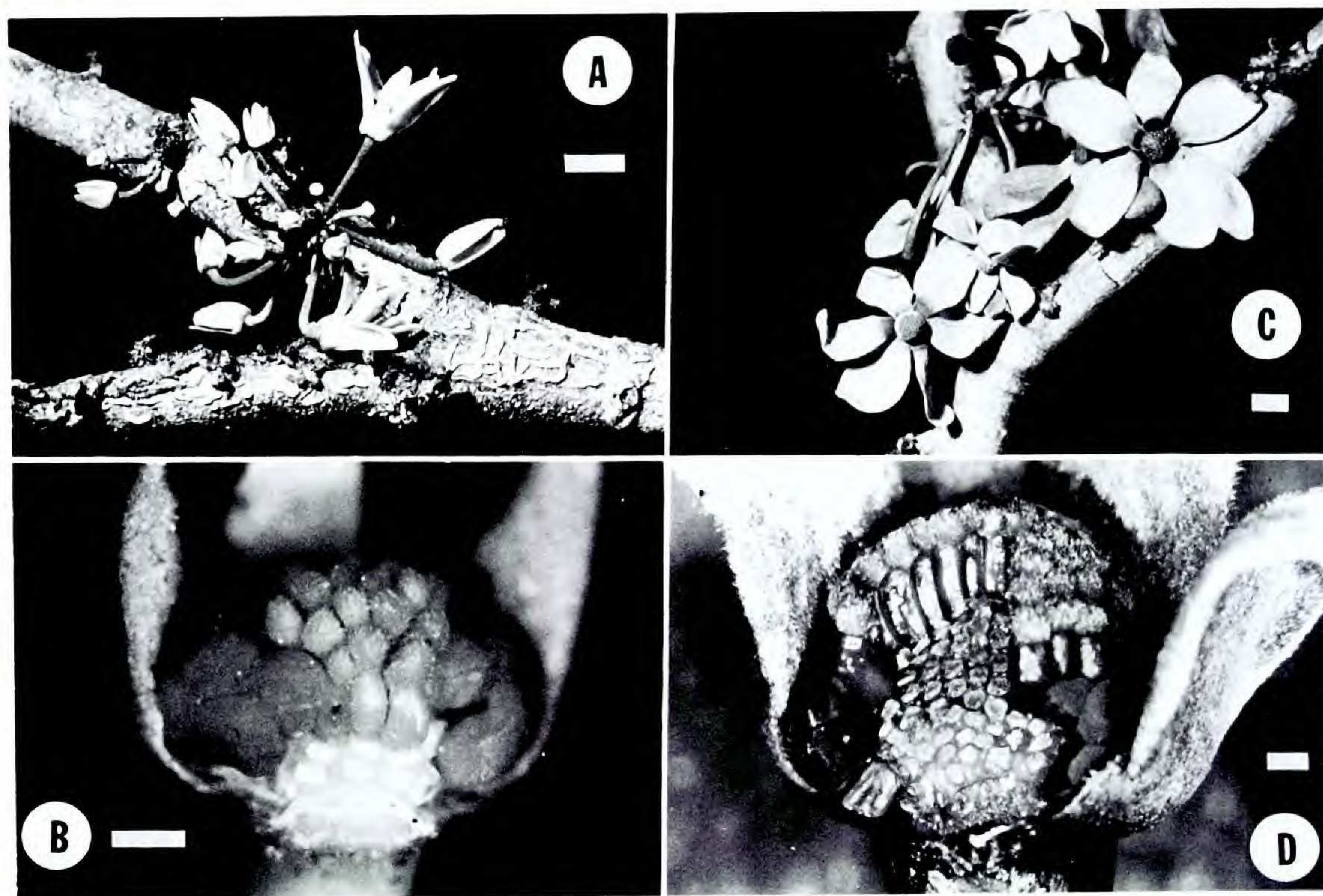


FIGURE 20. Flowers: A, *Polyalthia glauca* (Rogstad 939), different stages of development, scale bar = 5 mm; B, *P. glauca* (Rogstad 939), immature, few stamens removed, scale bar = 0.5 mm; C, *P. discolor* (Rogstad 814), later stages of development, scale bar = 5 mm; D, *P. discolor* (Rogstad 814), immature, some stamens and carpels removed, scale bar = 0.5 mm.

of *Polyalthia* (e.g., *P. cinnamomea* Hooker f. & Thomson, *P. lateriflora*, *P. longifolia*, *P. sclerophylla*), in which one or both portions are pubescent.

The carpels in the *Polyalthia hypoleuca* complex range from glabrous to tomentose, and all have a clearly visible adaxial stigmatic crest that can be detected even in fruit. The stigmas are always free and densely puberulent. They range from globose to elongate or clavate but are never obviously grooved, as they are in species of many annonaceous genera. The stigmas turn black and are presumably nonfunctional a few hours prior to anther dehiscence. Many of the floral characters described immediately above can be seen in FIGURES 18A and B, 19, and 20.

As the carpels mature, they turn from green to red, and then to purple-black at full ripeness. Within this complex only *Polyalthia sumatrana* has developing carpels that are green streaked with irregular red spots. Either the mature carpels and seeds are both ellipsoid, or they are globose with the seeds biconvex to lenticular. Species in which the mature carpels are ellipsoid have basal placentation and seeds with a strong longitudinal circumferential ridge, a basal micropyle, and a basal "aril scar"; those in which they are globose have ventral placentation and seeds with a longitudinal groove (or a very slight circumferentially raised area with a clear medial groove), a ventral micropyle, and no aril scar. All species of the group have seeds with rumination needles; they have predominantly one-seeded mature carpels (thus their placement in sect.



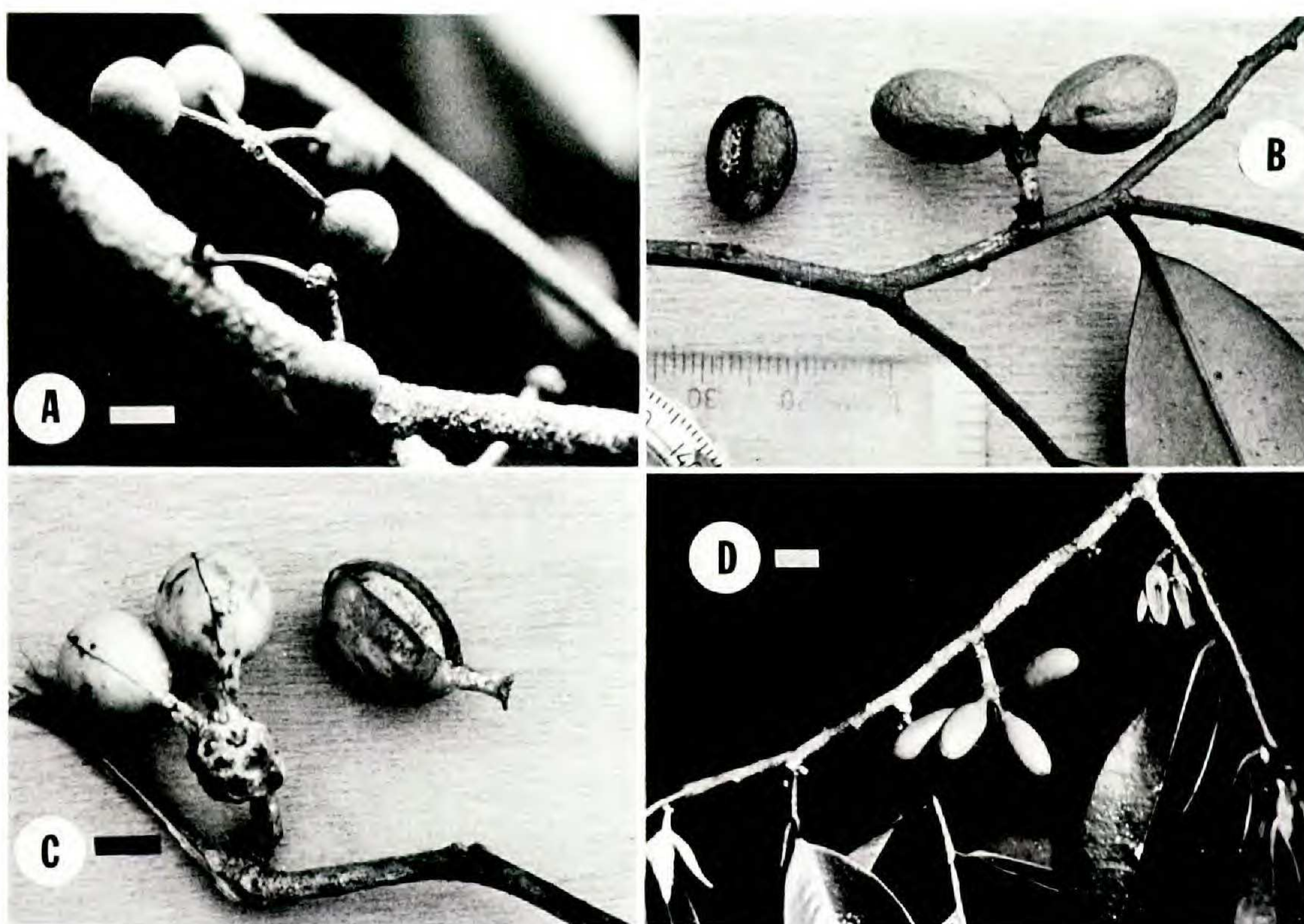


FIGURE 21. Near-mature fruits of members of *Polyalthia hypoleuca* complex: A, *P. glauca* (Rogstad 939); B, *P. hypoleuca* (Rogstad 912); C, *P. sumatrana* (Rogstad 508); D, *P. multinervis* (Rogstad 813). Scale bars = 1 cm.

Monoon by most authors), although occasional ones containing two seeds are found. For example, of 183 mature carpels of *P. glauca* sampled at Pasoh, 3.3 percent were two seeded, and most of these seeds germinated. Many of the above-described fruit and seed characters can be seen in FIGURES 7B–D, 8, and 21.

The four species for which chromosomes have been counted (*Polyalthia glauca*, *P. discolor*, *P. hypoleuca*, and *P. multinervis*) are all  $2n = 18$  (Rogstad, in prep. c).

One gains the impression from the relative number of times that each species of the *Polyalthia hypoleuca* complex has been collected that *P. sumatrana* must grow more abundantly than the others. However, the greater number of sheets of *P. sumatrana* is probably due to the fact that this species is the smallest tree in the group. Kochummen (1972) has stated that *P. glauca* is a rare species, but at Pasoh Forest Reserve, peninsular Malaysia, I found it growing in about equal density to *P. sumatrana*, although in much more restricted habitats and to much greater heights. Drawing conclusions about species distributions and relative abundance from herbarium materials alone can be misleading.

A specimen of *Polyalthia sumatrana* (Austin Cuadra A 2118, A) has a black fungus growing in circular colonies on the leaves. An annotation indicates that this fungus is *Meliola polyalthiae* Hansf. I have several times seen this fungus growing on *P. hypoleuca*, *P. sumatrana*, and most frequently *P. glauca* (in the last species, most of the leaves of an individual can be infected).



### Keys to the Species of the *Polyalthia hypoleuca* Complex

Due to the large amount of overlap of vegetative characters, no strictly vegetative key is presented here.

The morphometric analyses yielded suites of characters by which each species could be distinguished, but their use in entirety would make a key overly complex. I have thus attempted to construct keys based on important, commonly present characters that are relatively easy to determine. Most specimens have only flowers or fruits, so separate keys are provided for each contingency. The ranges of character dimensions have been obtained from the complete data sets that were used in the character-variation analyses reported above.

Although most of the characters used in the keys have been measured from dried herbarium specimens, these keys and the information provided in the species descriptions can also be used on fresh or fixed specimens. For example, the most useful characters for distinguishing fresh material are those unaffected by shrinkage; these include, for flowers, the number of stamens and carpels, the stamen/carpel quotient, the tomentum on the pedicel, the shape of the stigma, and the nature of the inflorescences, and for fruits, the shape of the mature carpels, the shape, circumferential ring, and nature of the aril area of the seeds, the pubescence (or lack thereof) on the pedicel, and the nature of the infructescence. However, it should be noted that mature specimens of *Polyalthia glauca* flowers that were first measured fresh shrank ca. 25–30 percent upon drying, with petals shrinking about 40–45 percent. Herbarium-specimen characters and label-note information that can be used to assess the maturity of flowers and fruits were given above in the discussion of how specimens were chosen for the morphometric analyses.

#### Key for Flowering Material

1. Stigmas elongate, 65–100% length of carpels, those in outermost ring of carpels bent at least 30° out from floral axis; inflorescences borne on branches, always below the leaves, arising mainly from tubercles, each with 1 terminal flower, this borne on extremely reduced peduncle ( $\leq 1.1$  mm long) bearing no other flowers or buds.
  2. Pedicels glabrous, young shoots glabrous to very sparsely pubescent; laminas narrowly elliptic, 2.5–7 cm wide, width/length quotient 0.24–0.34. . . . . 1. *P. glauca*.
  2. Pedicels and young shoots moderately to densely tomentose with short, rust-colored hairs; laminas usually elliptic to widely elliptic, 7–11.3 cm wide, width/length quotient 0.34–0.44. . . . . 2. *P. ovalifolia*.
1. Stigmas usually globose, not exceeding 64% of carpel length, if slightly elongate then those of outermost ring of carpels not strongly bent away from floral axis; inflorescences arising either both at and below present leaves (then lacking well-developed tubercles, with very reduced peduncle bearing only 1 terminal flower) or exclusively below the leaves and from tubercles (then usually with peduncle 1.1–11 mm long bearing lateral flowers or resting buds).
  3. Pedicels 7.5–50 mm long; stamens  $> 55$ ; carpels  $> 12$  (possibly very rarely  $\leq 12$  in *P. sumatrana*).
  4. Outer petals narrowly elliptic to elliptic (width/length quotient  $> 0.2$ ), with dense tomentum on adaxial surface beginning on basal  $\frac{1}{3}$ ; carpel/stamen quotient  $> 0.3$ ; inflorescences borne on branches below the leaves, arising from



- tubercles, with peduncle bearing lateral developing flowers or resting buds. . . . . 3. *P. discolor*.
4. Outer petals linear to narrowly elliptic (width/length quotient  $< 0.2$ ), with moderate to sparse tomentum on adaxial surface absent from at least basal  $\frac{1}{3}$ ; carpel/stamen quotient  $< 0.3$ ; inflorescences both from foliate axils and borne on branches below the leaves, well-developed tubercles lacking, the peduncles extremely reduced, bearing 1 terminal flower and no lateral buds. . . . . 4. *P. sumatrana*.
3. Pedicels  $< 7.5$  mm long; stamens  $< 55$ ; carpels generally  $< 12$ .
5. Pedicels moderately to densely tomentose; collected only west of New Guinea. . . . . 5. *P. hypoleuca*.
5. Pedicels glabrous (or very sparsely pubescent); collected only in Papua New Guinea. . . . . 6. *P. multinervis*.

Key for Fruiting Material

1. Distal portion of mature carpels globose; placentation ventral; seed(s) biconvex-lenticular, often with irregular indentations on surface, with longitudinal circumferential groove (this occasionally running medially within slightly raised circumferential area), no aril scar detectable.
2. Pedicels and youngest shoots with moderate to dense, short, rusty tomentum; laminae usually elliptic to widely elliptic, 7–11.3 cm wide, width/length quotient 0.34–0.44. . . . . 2. *P. ovalifolia*.
2. Pedicels glabrous, youngest shoots moderately pubescent at most; laminae narrowly elliptic, 2.5–7 cm wide, width/length quotient 0.24–0.34.
3. Stamen scars  $> 50$ ; mature carpels with stalks  $> 13$  mm long. . . . . 3. *P. discolor*.
3. Stamen scars  $< 45$ ; mature carpels with stalks  $< 13$  mm long. . . . . 1. *P. glauca*.
1. Distal portion of mature carpels ellipsoid; placentation basal; seeds ellipsoid, never with irregular indentations on surface, with strong longitudinal circumferential ridge, aril scar easily detectable.
4. Pedicels  $> 9$  mm long; stamen scars  $> 50$ . . . . . 4. *P. sumatrana*.
4. Pedicels  $< 9$  mm long; stamen scars  $< 50$ .
5. Pedicels moderately to densely tomentose; collected only west of New Guinea. . . . . 5. *P. hypoleuca*.
5. Pedicels glabrous (or very sparsely pubescent); collected only in Papua New Guinea. . . . . 6. *P. multinervis*.

Species Accounts

As with the characters used in the keys, those included in the species descriptions are taken largely from the data sets of mature floral or fruit characters used in the morphometric analyses. These data were collected from dried herbarium specimens (exceptions are noted). The minimum and maximum values of most continuous characters will be given for each species, followed in parentheses by the mean, the standard deviation, and the number of specimens for which the character could be evaluated. For noncontinuous characters, all specimens have the noted trait unless a percentage breakdown is given. In the latter case, the total number of specimens evaluated for the character will be given. Mean values, standard deviations, and number of herbarium specimens used are not reported when the last figure is less than ten.

Rather than listing all of the specimens I have examined, I give only selected



ones that illustrate the range of locations and of morphology for each species; all specimens used in the morphometric analyses are included. A “finders list” of all the specimens I have examined is on deposit with the Botany Libraries of Harvard University, and a copy of it will be sent upon request. Most information given for specimens should be self explanatory, with two exceptions. First, where it is not clear whether a label identification number refers to a collector or to the distributing institution, I have given the collector’s name or the institutional abbreviation in brackets. Second, a designation as to whether I classified the specimen on the basis of flowers (fl), fruits (fr), or both (fl+fr) is given immediately following the identification number for each specimen; sterile specimens are also indicated (st). If these designations are in capital letters, the specimen has been included in the data sets for the morphometric analyses. Note, however, that different specimens are missing values for different characters or are immature, so all of the specimens included in the data sets are not used in all of the data analyses presented above.

Local or common names applied to the species as recorded by collectors are listed alphabetically for each species. Different spellings that obviously refer to the same name are listed separately. A general location (or locations, if a name is widespread) is given with each name, with more precise information available in the list of selected specimens for each species.

Short descriptions of the habitat ecology are given, but these only very briefly summarize the results of more detailed investigations into comparative habitat ecology, seedling ecology, and floral biology of several species of this group, a full description of which will be detailed subsequently (Rogstad, in prep. a, b).

1. ***Polyalthia glauca*** (Hassk.) Mueller, Descr. Notes Papuan Pl. App. 95. 1877, non Boerlage (1899); *Uvaria glauca* Hassk. Flora **25**(Beibl. 2): 31. 1842; *Guatteria glauca* (Hassk.) Miq. Fl. Ned. Ind. **1**: 49. 1855; *Monoon glaucum* (Hassk.) Miq. Ann. Mus. Bot. Lugduno-Batavum **2**: 19. 1865. TYPE: *Hasskarl s.n.* (possibly marked “nom. sund. Kaju tinjang” and/or “Arbor in m. Roeboet”) (n.v.).

FIGURES 2A, B; 3B, C; 4C; 6C, D; 8D; 18C; 20A, B; 21A.

*Guatteria hypoleuca* Miq. Fl. Ned. Ind., Eerste Bijv. 381. 1861. TYPE: [Sumatra] Priaman, Madang Poelo, *Diepenhorst 2095* (U).

“*Unona hypoglauca* Miq.” ex Hooker f. & Thomson, Fl. Brit. India **1**: 63. 1872, nomen nudum.

*Unona merrittii* Merr. Philipp. J. Sci. C. **1**: 190. 1906; *Polyalthia merrittii* (Merr.) Merr. Philipp. J. Sci. C. **10**: 250. 1915. TYPE: Philippines, Mindoro, Bongabong River, February 23, 1906, *Whitford 1447* (n.v.).

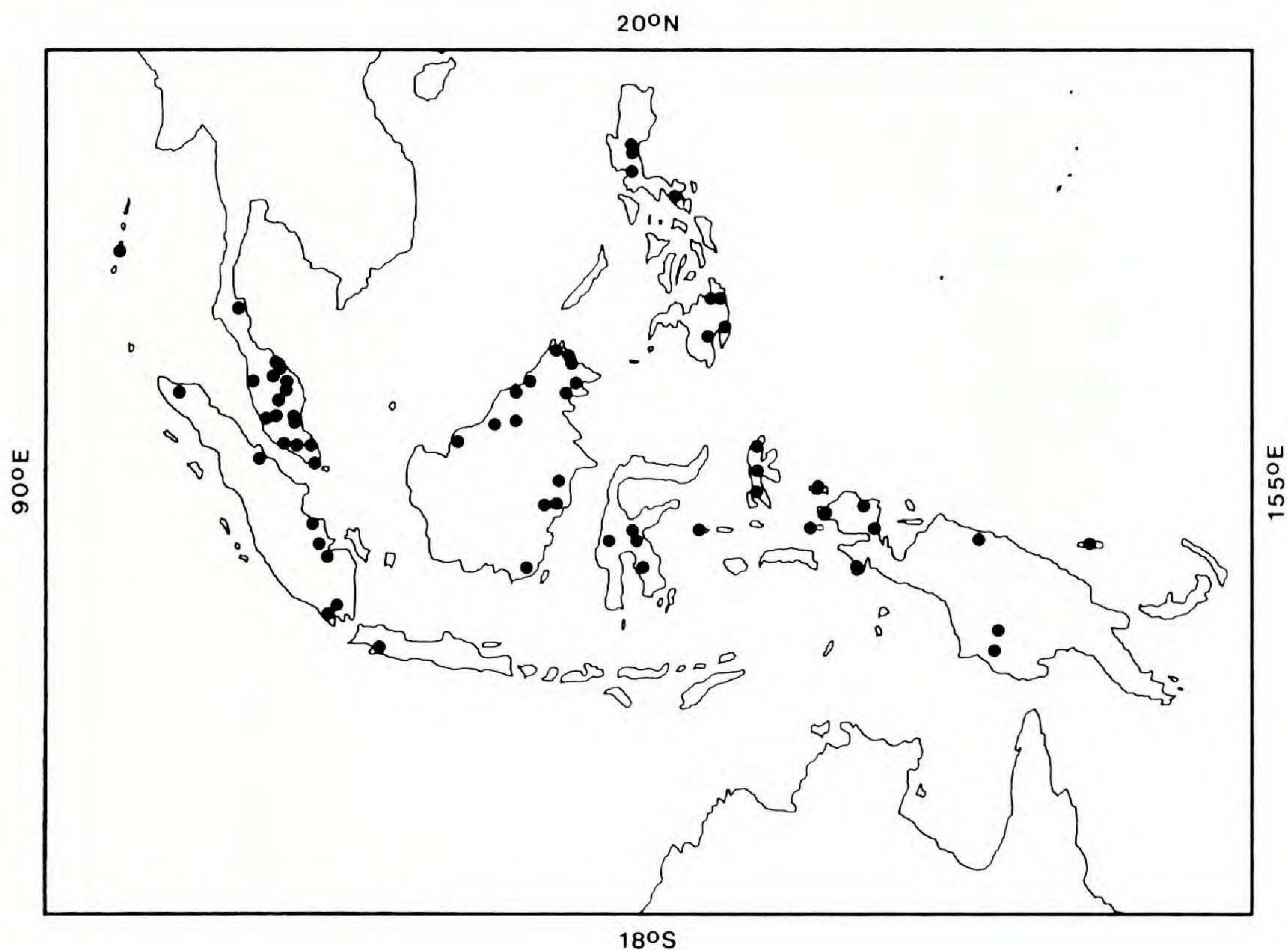
*Polyalthia parkinsonii* Hutch. Bull. Misc. Inform. **1917**: 25. 1917. SYNTYPES: India, Andaman Islands, Long Island, Feb., *Parkinson 943* (fr) (K); without precise locality, Dec., *Parkinson 765* (fl) (K), *794* (fl) (K).

Tree to 45 m tall, DBH to 56 cm; trunk often fluted at base; pneumatophores (except at drier sites) arising from below soil 0.5–1.5 m from base, ascending up to 0.7 m, then recurving to reenter soil, sometimes emerging again farther away, extending up to 8 m from tree base; bark white, smooth on younger trees and branches but papery and flaking, revealing red, papery and flaking bark



above height of 3 m or more on boles of many older trees; hoop marks prominent even on lower portions of bole; slash on larger trees revealing phloem rays separated from surface by 2 mm or more of woody matrix, phloem-ray apices 0.5–1.5 mm apart. Twigs with bark white, often having small red spots throughout, youngest growth glabrous (39%) to slightly tomentose (61%;  $n = 31$ ). Leaves with young petiole 3–8 (5.8, 1.4, 31) mm long, glabrous to moderately tomentose abaxially; lamina narrowly elliptic to elliptic, 9–22 (14.3, 3.3, 31)  $\times$  2.5–7 (4.4, 1.1, 31) cm, the apex acuminate to apiculate, 0.3–2.1 (0.9, 0.4, 31) cm long, the base rounded to acute, the secondary veins 13 to 39 (21.5, 6.2, 31) per side, occasionally looping more or less regularly to form weak intramarginal vein; leaves when fresh weakly conduplicate with abaxial surface bright white. Inflorescences borne on branches below leaves, arising predominantly from tubercles, 2 to 15 per tubercle; peduncle extremely reduced, 0.2–1.1 (0.5, 0.3, 23) mm long, usually with only 1 terminal flower developing, lateral floral buds and developing flowers absent; bracts 1 to 3, irregularly oriented with respect to branch axis. Flowers with pedicel 7–29 (18.1, 6, 23) mm long, 0.2–0.8 (0.6, 0.16, 23) mm wide at base and 0.6–1.4 (0.9, 0.19, 23) mm at apex, glabrous (90%) to sparsely pubescent (10%;  $n = 25$ ); bract sometimes (48%;  $n = 23$ ) present, 4–16 (8.3, 3.2, 11) mm above articulation. Sepals triangular, 0.6–1.9 (1, 0.28, 23) mm long, abaxially moderately (22%) to densely (78%;  $n = 23$ ) tomentose, infrequently caducous at floral maturity. Petals linear (91%) to basally clawed with distal portion linear (9%;  $n = 23$ ); outer petals 7–18 (10.4, 3.2, 23)  $\times$  1–4.5 (2.2, 1, 23) mm, with the pubescence beginning adaxially on basal (83%) or middle (17%;  $n = 23$ )  $\frac{1}{3}$ , sparse throughout (9%), moderate throughout (21%), dense throughout (52%), or sparse throughout except abaxially at base where dense (17%;  $n = 23$ ), the midvein generally not visible abaxially; inner petals 6–18 (10.9, 3.5, 23)  $\times$  0.9–3.5 (1.8, 0.7, 23) mm; all petals yellow when stigmas become receptive, very fragrant (pleasant–sickly sweet; similar to *Cananga*), turning purplish sepia when anthers dehisce. Torus 0.2–0.8 (0.47, 0.18, 23)  $\times$  1.1–2 (1.5, 0.26, 23) mm, gynoeceal portion concave (4.4%), flat (56.5%), or convex (39.1%;  $n = 23$ ). Androeceum 2–3 (2.5, 0.3, 23)  $\times$  0.5–1.4 (1.1, 0.2, 23) mm; stamens 15 to 31 (23.8, 3.6, 23), 0.5–1 (0.78, 0.12, 23)  $\times$  0.7–0.9 (0.77, 0.08, 23) mm. Gynoeceum 1–2.8 (1.9, 0.4, 23) mm across; carpels 10 to 25 (17.7, 3.1, 23), 0.6–1 (0.78, 0.14, 23) mm long, glabrous (100%;  $n = 23$ ); stigmas elongate, clavate, 0.4–1.1 (0.6, 0.18, 23) mm long, those of outermost ring reflexed at least 30° out from floral axis. Immature carpels green, turning red, finally blackish purple, the pericarp then soft and fleshy (juice laden), with sweet to bitter-sweet taste. Mature, dry fruits with pedicel 8–35 (22.8, 6.4, 33) mm long, 1.1–3.2 (1.8, 0.56, 33) mm in diameter at apex, glabrous (97%) or sparsely pubescent (3%;  $n = 33$ ); stamen scars  $< 40$  (100%;  $n = 21$ ); carpels with the stalk 3–16 (7.9, 2.7, 31)  $\times$  1.2–2.7 (1.9, 0.39, 31) mm, the seed-bearing portion globose, 9–25 (15, 3.4, 32)  $\times$  11–25 (15.4, 3.3, 32) mm, not ridged, rounded at apex; fruit wall  $< 1$  mm thick, deep red to black. Placentation ventral at maturity. Seed(s) 1 (or 2) per mature carpel, biconvex-lenticular, with circumferential groove (this occasionally within slightly raised area), the aril scar lacking, the testa deep brown to black (often green when fresh), smooth to





MAP 2. Distribution of *Polyalthia glauca*.

finely pitted, often irregularly indented in both fresh and dried seeds; rumination acicular.

**DISTRIBUTION.** Andaman Islands, southern Thailand, peninsular Malaysia, Sumatra, Borneo, New Guinea, Admiralty Islands (MAP 2).

**SELECTED SPECIMENS SEEN.** **India.** ANDAMAN ISLANDS: sine loco, *Parkinson* 765 (FL) (κ), 794 (FL) (κ); Bom-ling-la, *Parkinson* 943 (FR) (κ). **Thailand:** Khao Tha Phet F.R., Surat Thani, 40 m alt., *Rogstad* 841 (fr) (A, BKF). **Malaysia.** TRENGGANU: Kiat, Sungei Nerus, Kuala Trengganu, *SFN* 40915 (FR) (KEP, L, SING). PERAK: Changkat Jong F.R., 100 m alt., *FRI* 5611 (fr) (KEP). KELANTAN: Ulu S. Aring, near K. Tapah, *FRI* 4485 (FR) (KEP, SAR); Sungai Lebir, Kuala Sepia, *FRI* 7038 (FR) (A, KEP, L, SAR). PAHANG: Tasek Bera, near Fort Isikandar, 45 m alt., *FRI* 3972 (FR) (A, KEP); Taman Negara, 75 m alt., *FRI* 14327 (FR) (A, κ, KEP, L), *FRI* 14438 (FR) (A, KEP, L); Kuala Lompat Game Reserve, Kuala Krau, *FRI* 25108 (FR) (KEP). NEGRI SEMBILAN: Pasoh F.R., near Simpang Pertang, *Rogstad* 939, 944, 945, 966 (all FL) (all A); Perhutian Tinggi(?), *Ridley*(?) 10030 (fr) (κ); Pasoh F.R., *FRI* 27582 (FL+fr) (FRI). JOHORE: Kuala Sedili, *Kadim & Noor* 195 (fr) (A, SING); Sungai Sedili, Mawai, *SFN* 29274 (FR) (A, SAR, SING); Ayer Hitam F.R., 50 m alt., *KEP* 98248 (A, KEP). SARAWAK: Semengoh Arboretum, Kuching, 15 m alt., *Brain anak Tada s.n.* (FR) (A, KEP, L, SAR); Ulu Mayeng, Kakus, 60 m alt., *S* 21710 (FR) (SAR, SING). SABAH: Kelumpang Balong, Tawau, 915 m, *SAN* 18520 (FR) (L, SAN); 5.5 mi NE of Ranau, 472 m alt., *SAN* 28987 (FL) (L, SAN); Biah trail, Sapong Estate, Tenom Distr., 300 m alt., *SAN* 50232 [*Sadaw*] (FR) (SAN); Crocker Range F.R., Rayoh, Tenom Distr., *SAN* 78396 (FR) (KEP, SAN, SAR); Gum-Gum F.R., 16 mi N of Sandakan, 140 m alt., *SAN* 90945 (FL) (SAN); Sogo-Sogo, 11 mi from K. Tongod, *SAN* 91121 (FR) (SAN). **Singapore:** Mandai Road, *SFN* 34448 (FR) (KEP, SING); Mondai Road, *SFN* 37120 (FR)



(KEP, SING). **Philippines.** LUZON: Baler, Principe Prov., *Merrill 1031* (FR) (PNH, US). Camarines Prov., *FB 10475* [Curran] (FR) (PNH, US); Nueva Vizcaya, Luzon Prov., *FB 28532* (FR) (PNH, US); Casiguran Tayabas Prov., *BS 45271* (FR) (A, K, PNH, US). SIBUYAN: Magellanes (Mt. Giting-Giting), Capiz Prov., *Elmer 12449* (FR) (A, US). MINDANAO: Mt. Hamiguitan, Davao Prov., 600 m alt., *Edaño 1688* (FL) (A, PNH); Butuan Subprov., *FB 20757* (FR) (PNH, US). **Indonesia.** SUMATRA AND ADJACENT ISLANDS: Palembang, 20 m alt., *Grashoff 820* (FR) (BO, L); Tg. Djawidjawi, P. Mendol, Selatpandjang, 5 m alt., *bb 21461* (FR) (A, BO, L); Belimbing, 6 m alt., *bb 28490* (FR) (BO, L); Djepara, NE Lampung, 20 m alt., *bb 35755* (FR) (BO, L). KALIMANTAN: Bangarmassing, *Motley 932* (FL) (K); Tdg. Bangko region, near mouth of Mahakam R., 20 m alt., *Kostermans 7193* (FR) (A, BO, L); Nunukan Is. (northern part), *Kostermans 8954* (FL+fr) (A, BO, K); Sg. Mentawir region, near Mentawir Village, Balikpapan Distr., *Kostermans 10022* (FL) (BO, KEP). JAVA AND ADJACENT ISLANDS: Ujung Kulon Reserve, Mt. Pajung, 300 m alt., *Kostermans c. s. (UNESCO) 165* (FR) (BO, L). CELEBES: En Ond Malili, *Cel./2.-446* (FL+FR) (A, BO); Malili, *Cel./2.-491* (FR) (BO, K). MOLUCCAS: G. Permatang, Sangowo R., Morotai, *Kostermans 927* (fl+FR) (A, BO, LAE); Tiloppe, Weda, 25 m alt., *bb 24853* (FR) (A, BO, L); Morotai, Subdistr. Tobelo Totodokoe, 30 m alt., *bb 33737* (FR) (A, BO, K), *bb 33750* (FR) (BO, L). IRIAN JAYA: Sorong, Fakal, bank of Kasim R., Misool, *Pleyte 859* (FL+fr) (A, BO, SING); Subdistr. Ransiki, Meos Waar Is., 5 m alt., *BW 1214* (FR) (A, SING); Hollandia [Jayapura], 40 m alt., *BW 4817* (FR) (A, LAE); Radjah Ampat, Lupintol Village, Waigeo Is., 40 m alt., *Van Royen 5481* (FR) (L, SING); Adi Is., Fak-Fak Div., 25 m alt., *BW 10173* (FL+fr) (A, Boswezen); sine loco, *Zippiel* [Zippelius] *s.n.* (FL) (A, L). **Papua New Guinea and adjacent islands.** WESTERN PROVINCE: Agu R. branch of middle Fly R., near Mipan Village, 30 m alt., *Pullen 7394* (FL+fr) (A, CANB, L); Lake Daviumbu, middle Fly R., *Brass 7622* (FL) (A). MANUS PROVINCE: above Derimbat Village, Admiralty Islands, 100 m alt., *LAE 59246* (FR) (A, LAE, US).

REGIONAL NAMES. "Lanotan," Ma language, Davao Prov., Philippines, *G. E. Edaño 1688*. "Lulusan sowong," language?, Ranau Distr., Sabah, *SAN 28987*. "Manitan," language?, Selangor, peninsular Malaysia, *KEP 28833*. "Mempisang" (a general name for several Annonaceae), Malay language, SE Kelantan, peninsular Malaysia, *FRI 7038*. "Minakoe," Manikiong language, Meos Waar Is., New Guinea, *BW 1214*. "Paroe," Selogof language, Waigeo Is., New Guinea, *Van Royen 5481*. "Pisang-pisang" (a general name for several Annonaceae), Malay language, Tawau, Sabah, *SAN 18520*. "Saselo," language?, Morotai, Moluccas, *bb 33737*. "Songyu" (a general name for several Annonaceae), (local?) Thai language, Surat Thani, Thailand, *Rogstad 841*.

LOCAL USE. *Polyalthia glauca* is thought to be the best source of firewood in the northern region of Sarawak (*Motley 932*). The wood of larger *P. glauca* trees may also be used for crate and toy construction in peninsular Malaysia (Timber Utilization Chart, Forest Research Institute, Kepong, Selangor, Malaysia).

ECOLOGY. Specimens have been collected from sea level to 915 m alt. Of species in the *Polyalthia hypoleuca* complex, *P. glauca* has the widest geographic range. Although occasional specimens of this species are marked as collected from hillsides, the bulk of the herbarium notations, as well as my own observations, indicate that this species most frequently grows in saturated soils along streams, at seasonally or permanently inundated sites, or in peat swamps. It can be quite common (eight to 15 mature individuals/ha) in such habitats. Exceptions to this pattern can be found in drier regions at the boundaries of the species range (e.g., Thailand; *Rogstad 841*). Mature trees of this species occupy the middle



to upper canopy. At Pasoh F.R., peninsular Malaysia, flowering can occur, with varying intensity, at least twice per year. Each period is immediately preceded by the initiation of growth of new branches and leaves and may include four (or more?) separate ten- to 14-day waves of flowering.

COMMENTS. I have been unable to locate the type specimen for *Polyalthia glauca* at A, B, BO, F, GH, K, KEP, L, MO, P, SAN, SAR, SING, U, US, or WRSL, and neotypification may be necessary. A type specimen for *P. merrittii* has also not been found at A, B, BO, F, GH, K, KEP, L, LY, MO, P, PNH, SING, U, UC, US, or WRSL.

Miquel's description of *Guatteria hypoleuca*, and the type specimen noted for this name in the synonymy, are both beyond doubt *Polyalthia glauca*. Hooker and Thomson (1872), in describing *Polyalthia hypoleuca*, did not mention *Guatteria hypoleuca* anywhere in the text, but they did compare their newly described species to "*Unona hypoglauca* Miq." This latter name has not been published elsewhere. A syntype of *P. glauca* (at K) is labeled *Unona hypoglauca* in an unidentified hand, and *Guatteria hypoglauca* by Miquel. This specimen must be responsible for the reference of Hooker and Thomson above and is thus the probable source for the *nomen nudum*.

Individuals of *Polyalthia glauca* are often easy to find in poorly drained areas due to the bright red bark that develops on the upper bole of many, but not all, trees (the flaking bark of this species makes it a difficult subject for research because it is often impossible to climb the slippery trunks) and the pneumatophores that may emerge from the soil within a meter or so of the base of the bole, then curve back to and reenter the soil, often again emerging and reentering the soil at a greater distance. A pneumatophore system of one tree may extend up to 8 m from the base of the tree, and because the older pneumatophores have the white bark characteristic of the *P. hypoleuca* complex, they are easily spotted in the field. The extension growth of emergent pneumatophores has an interesting pattern of periodicity marked by annular scars (see FIGURE 6D). Within the *P. hypoleuca* complex, such pneumatophores have been found only in *P. glauca* individuals growing at poorly drained sites.

Sinclair (1955) implicitly recognized *Polyalthia parkinsonii*, although he did not treat it in detail since he thought it occurred outside of the geographic range under consideration. He did suggest, however, that the entity of the *P. hypoleuca* complex found in Burma and the Andaman Islands by Kurz (1874) was actually *P. parkinsonii*, rather than *P. sumatrana*, as the latter author believed. Since Kurz did not list the specimens on which he based his report (and I have been unable to find any specimens of *P. sumatrana* collected in Burma or the Andamans), it is likely that he was dealing with specimens more properly assigned to *P. glauca*. This conclusion finds support in the fact that to date, only *P. glauca* is known from Thailand (Rogstad 841), thus being the only species of the complex collected to the north and west of Sumatra and peninsular Malaysia.

Within the *Polyalthia hypoleuca* complex, specimens of *P. glauca* are most likely to be confused with *P. ovalifolia* (restricted to Borneo) or *P. discolor* (restricted to Papua New Guinea); see the discussion under the latter two species.

The curious irregular indentations of the seed surface often seen in herbarium



specimens of this species can also be observed in fresh material (see FIGURE 8D). All of the more than 230 seeds germinated at Pasoh Forest Reserve had them. Such indentations were well developed in all herbarium specimens with mature fruit collected from peninsular Malaysia, Sumatra, and the Andamans, but they are less prominent in collections from Borneo, present in only two of the four collections from the Philippines, and completely lacking in specimens from New Guinea and the Admiralty Islands. In seeds where the indentations are lacking, the rumination needles characteristic of the *Polyalthia hypoleuca* complex occasionally become slightly broadened near the longitudinal circumferential groove.

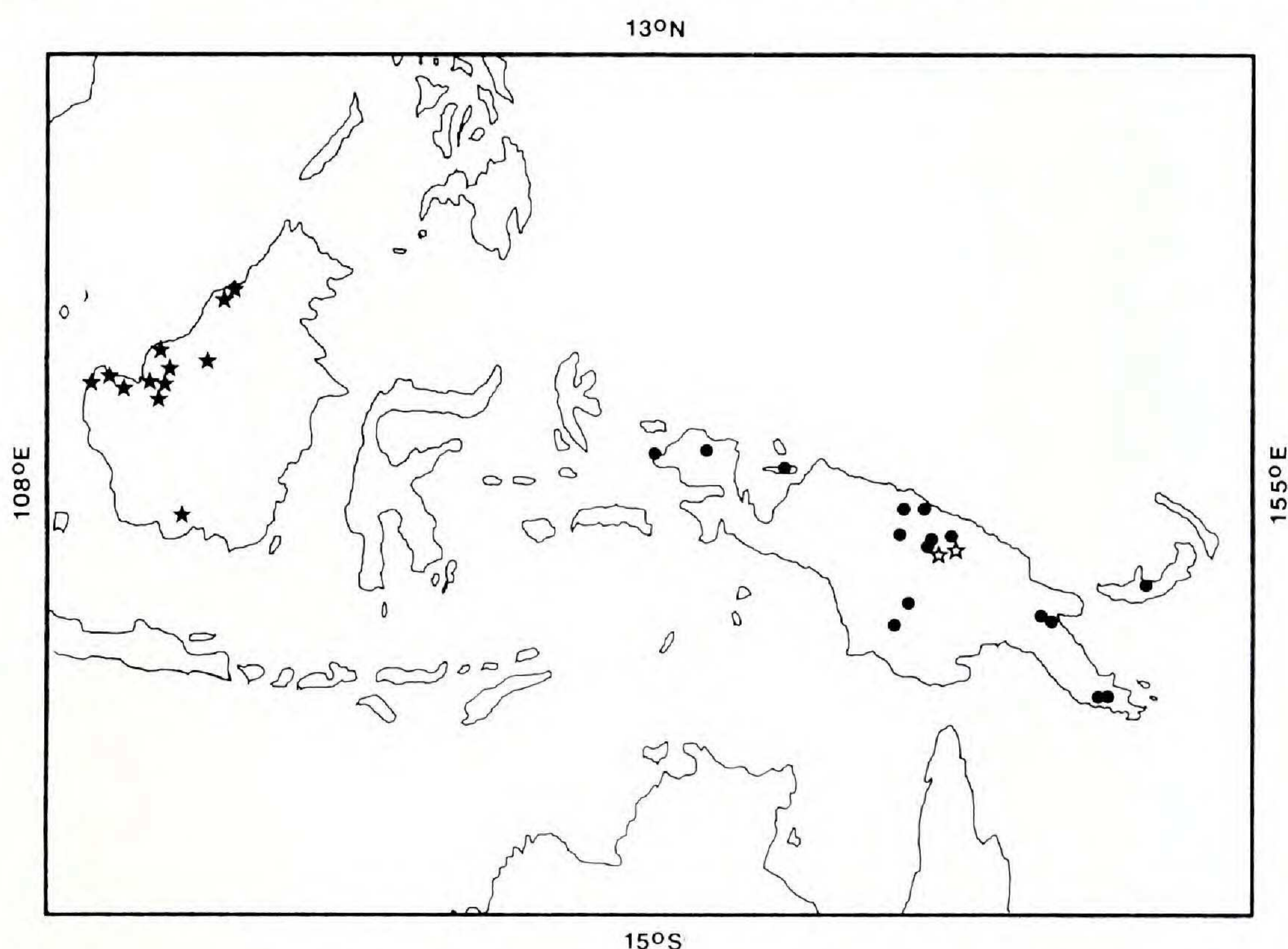
## 2. *Polyalthia ovalifolia* S. H. Rogstad, sp. nov.

FIGURE 3A.

*P. glauca* affinis, sed in ramulis novellis et in pedicellis indumento moderate vel dense tomentoso praeditis (haud moderate vel dense tomentoso in *P. glauca*); foliis grandioribus (19–26 × 7–11.3 cm versus 9–22 × 2.6–7 cm in *P. glauca*), latioribus (foliis latitudo/longitudo ratio plerumque 0.34–0.44 versus 0.24–0.34 in *P. glauca*), et magis coriaceis, differt.

Tree to 25 m tall, DBH to 55 cm; trunk often fluted at base; pneumatophores absent; bark white, smooth on younger trees and branches, becoming white mixed with yellow when older; hoop marks prominent even on lower portions of bole; slash on larger trees revealing phloem rays separated from surface by 2 mm or more of woody matrix, phloem-ray apices 0.5–1.5 mm apart. Twigs with bark white to pale yellow-white, youngest growth always with dense, short, rusty tomentum ( $n = 20$ ). Leaves with young petiole 6–10 (8, 1.2, 12) mm long, moderately to densely tomentose abaxially; lamina elliptic to widely elliptic, 19–26 (22.5, 1.5, 12) × 7–11.3 (9.6, 1.1, 12) cm, the apex acuminate to apiculate, 0.8–1.7 (1.1, 0.3, 12) cm long, the base rounded, the secondary veins 21 to 36 (29.6, 4.7, 12) per side, wavering and not forming strong intramarginal vein; leaves when fresh flat, with abaxial surface bright white. Inflorescences borne on branches below leaves, arising predominantly from tubercles, up to 20 per tubercle; peduncle extremely reduced, 0.7–2.1 mm long, usually with only 1 terminal flower developing, lateral floral buds and developing flowers absent; bracts 1 to 3, irregularly oriented with respect to branch axis. Flowers with pedicel 10–18 mm long, 0.7–1.2 mm wide at base and 1–1.5 mm at apex, with dense, short, rusty tomentum; bract 1.1–8 mm above articulation. Sepals triangular, 0.9–1.9 mm long, abaxially densely tomentose, infrequently caducous at floral maturity. Petals linear; outer petals 7.5–13 × 2–3.1 mm, the pubescence beginning adaxially on basal  $\frac{1}{3}$ , moderate throughout except abaxially at base where dense, or dense throughout, the midvein generally not visible abaxially; inner ones 8.5–13 × 2–2.2 mm; all petals (and sepals) pale orange, strongly fragrant (*S 12401*), deep burgundy-red when dry. Torus 0.5–1.1 × 1.8–2.5 mm, gynoeceal portion convex. Androeceum 0.9–2 × 2.1–2.8 mm; stamens 26 to 36, 0.8–1 × 0.7–0.9 mm. Gynoeceum 2–2.1 mm across; carpels 20 to 27, 0.7–1.1 mm long, glabrous or with slight tuft of tomentum only on abaxial apex; stigmas elongate, clavate, 0.5–1.1 mm long, those of outermost ring reflexed at least 30° out from floral axis. Observations





MAP 3. Distributions of *Polyalthia discolor* (dots), *P. ovalifolia* (solid stars), and *P. multinervis* (open stars).

on immature carpels lacking. Mature, dry fruits (only 2 available) with pedicel 16–27 mm long, 2.2–2.4 mm in diameter at apex, with dense, short, rusty tomentum; stamen scars < 40; carpels with the stalk  $3\text{--}4 \times 1.7\text{--}1.9$  mm, the seed-bearing portion globose,  $15\text{--}19 \times 14\text{--}18$  mm, smooth, rounded at apex; fruit wall < 1 mm thick, deep red to black. Placentation ventral at maturity. Seed(s) 1 (or 2?) per mature carpel, biconvex-lenticular, with circumferential groove, the aril scar lacking, the testa deep brown to black, smooth to finely pitted, not irregularly indented; rumination needles occasionally slightly broadened.

TYPE. S. and E. Borneo, Sampit, 5 m alt., 09-20-1925, *Buwalda* [sheets may be marked *F. H. Endert*] 7797 (fl) (holotype, A; isotype, BO).

DISTRIBUTION. To date collected only from northwestern and southern Borneo (see MAP 3).

SELECTED SPECIMENS SEEN. **Malaysia.** SARAWAK: Maludan Peninsula, Tj. Keranji, Betong Distr., 3 m alt., *S* 12401 [*Anderson*] (FL) (BO, K, SAR); Setapok F.R., Kuching, 15 m alt., *S* 12967 [*Zen*] (FR) (SAR); Bako Natl. Park, near Kuching, *Rogstad* 842-845 (st) (A). **Brunei:** Badas F.R., 15 m alt., *S* 2226 (FL) (FRI, SAR, SING); Badas State Land, Kuala Belait, 13 m alt., *SAN* 17439 (FR) (A, KEP, SAN).

REGIONAL NAMES. “Dillah,” language?, above Sibu, Sarawak, *S* 2342. “Dilleh,” language?, Brunei, *S* 2226. “Riboei,” language?, Sampit, Kalimantan, *Buwalda*



(or Endert?) 7797. "Selaut telor," Malay language(?), Betong Distr., Sarawak, S 12401 [Anderson].

ECOLOGY. The highest recorded altitude for *Polyalthia ovalifolia* is 15 m above sea level, but the species is poorly collected. Rather dense populations (up to ten mature individuals/ha) were observed at Bako F.R., Sarawak, where they appeared to be restricted to areas of stunted forest (the closed kerangas (heath) forests of Brunig (1974); canopy at 20–25 m) that grow on sandy soils covered with a spongy root-humus mat (to 1 m thick). These stunted, closed forests yield black water drainage and are the only habitat where regeneration of this species was found to be occurring at Bako. While this soil formation is reminiscent of peat, it differs in that it appears on flat or gently sloping hilltops and is well drained. However, *P. ovalifolia* has also been collected in peat-swamp forests in Sarawak (S 12401 [Anderson]; S 12967 [Zen]), although I could not find it in the extensive peat swamp formations adjacent to the Baram River, and foresters working in these swamps (e.g., employees of Forescom Sarawak), when presented with leaves of this species, stated that they had not observed it there although they immediately recognized the leaves of *P. hypoleuca*, which grows abundantly in that region.

COMMENTS. There has been some confusion concerning the collector of the type specimen. Sheets at A and BO that agree in collection number, date, and specimen material indicate different collectors (E. H. Endert at A, Buwalda at BO). A comparison of the collecting itineraries (Van Steenis–Kruseman, 1950) indicates that Buwalda was the collector.

This species is most likely to be confused with *Polyalthia glauca*; specimens listed above have usually been identified as *P. glauca* by various workers, including Sinclair. *Polyalthia ovalifolia* differs consistently from *P. glauca* in having moderately to densely tomentose (vs. glabrous) pedicels in flower and fruit, more coriaceous, larger leaves (see FIGURES 3A and 9) that are elliptic to broadly elliptic (vs. narrowly elliptic to elliptic) and usually have a higher width/length quotient (0.34–0.44,  $n = 12$ , vs. 0.24–0.34,  $n = 31$ ;  $P < 0.05$ , unbalanced t-test), and young branches always (vs. rarely) with dense, short, rusty tomentum. Although the differences between these two species are not pronounced, they are constant, and no intermediates have yet been found. I have therefore recognized *P. ovalifolia* as a distinct species, although more material and field observations of both *P. ovalifolia* and *P. glauca* in Sarawak and southern Kalimantan are needed.

3. ***Polyalthia discolor*** Diels, Bot. Jahrb. Syst. **49**: 130, 1913. TYPE: Papua New Guinea, middle April River, Niksek Village area, 4°42'S, 142°32'E, 100–150 m alt., Sept. 16, 1984, Rogstad 814 (fl+fr) (neotype, A; isoneotypes, K, LAE). FIGURES 2C, D; 4B; 6B; 7B; 8C; 20C, D.

Tree to 35 m tall, DBH to 91 cm; trunk often fluted at base; pneumatophores absent; bark white, smooth on younger trees and branches, with very fine dots of red giving main bole reddish tinge, flaking papery patches scattered on older bark; hoop marks prominent even on lower portions of bole; slash on larger trees revealing phloem rays separated from surface by 2 mm or more of woody matrix, phloem-ray apices 0.5–1.5 mm apart. Twigs with bark white to pale



yellow-white, youngest stem growth glabrous (50%) or with moderately dense, short, rusty tomentum (50%;  $n = 20$ ). Leaves with young petiole 3–9 (6.4, 1.7, 14) mm long, glabrous (75%) to moderately tomentose (25%;  $n = 20$ ) abaxially; lamina narrowly elliptic to elliptic, 10.2–15.8 (13.1, 1.3, 14)  $\times$  3.3–5.1 (3.9, 0.55, 14) cm, the apex acuminate to apiculate, 0.4–1.1 (0.75, 0.2, 14) cm long; the base rounded to acute, the secondary veins 17 to 28 (23.3, 3.5, 14) per side, occasionally looping more or less regularly to form weak intramarginal vein; leaves when fresh slightly to strongly conduplicate, with abaxial surface bright white. Inflorescences borne on branches below leaves, arising predominantly from tubercles, up to 10 per tubercle; peduncle ca. 1.1–11 mm long, with up to 3 lateral flowers developing or with resting buds; bracts 1 to 7 (often subtending resting or developing bud), distichous, but irregularly oriented with respect to branch axis on different inflorescences of single tubercle. Flowers with pedicel 18–49 (29.2, 8.3, 11) mm long, 0.8–1.2 (0.94, 0.1, 11) mm wide at base and 1.1–2 (1.6, 0.3, 11) mm at apex, glabrous (75%;  $n = 12$ ), occasionally with sparse, short, rusty tomentum; bract always present ( $n = 11$ ), 2–18 (8.8, 4.9, 11) mm above articulation. Sepals triangular, 1.3–2.2 (1.7, 0.36, 11) mm long, moderately tomentose abaxially, infrequently caducous at floral maturity. Petals narrowly elliptic to elliptic to obovate, occasionally with constriction or narrowing in basal  $\frac{1}{3}$  or with distal portion slightly flared (or both); outer petals 16–32 (20, 5.7, 11)  $\times$  4.5–7.3 (5.8, 0.83, 11) mm, the pubescence always beginning adaxially on basal  $\frac{1}{3}$  ( $n = 20$ ), moderate throughout except abaxially at base where dense, or dense throughout, the midvein often visible; inner petals 14–38 (22.1, 8.8, 11)  $\times$  4–9 (5.4, 1.5, 11) mm; all petals red-purple basally, yellow distally, and noticeably sweet smelling when stigmas become receptive, turning purplish sepia, musky, and sickly sweet when anthers dehisce, rusty to deep burgundy-red when dry. Torus 0.8–1.4 (1, 0.16, 11)  $\times$  2.3–3.3 (2.8, 0.32, 11) mm, gynoecial portion flat (100%;  $n = 3$ ) or convex (100%;  $n = 8$ ). Androecium 1–2.5 (1.9, 0.4, 11)  $\times$  3.6–5.1 (4.5, 0.4, 11) mm; stamens 77 to 119 (95.3, 14, 11), 0.9–1.3  $\times$  0.6–0.9 mm ( $n = 11$ ). Gynoecium 2.3–4 (3.1, 0.5, 11) mm across; carpels 31 to 72 (48.2, 13.6, 11), 1–1.4 (1.14, 0.12, 11) mm long, glabrous (90%) or with slight tuft of tomentum only on abaxial apex (10%;  $n = 20$ ), the outermost ones slightly incurved, distal portion of abaxial surface exposed above androecium, with exposed region slightly swollen and often slightly darker; stigmas globose, 0.2–0.7 mm long (0.45, 0.13, 11) mm in diameter, those of outermost ring not reflexed away from floral axis. Immature carpels green, turning red, finally blackish purple, the pericarp then soft and fleshy (juice laden), with sweet to bitter-sweet taste and often chlorinelike odor. Mature, dry fruits with pedicel 24–50 (34.6, 7.2, 14) mm long, 2–4.5 (3, 0.8, 14) mm in diameter at apex, glabrous (100%;  $n = 14$ ); stamen scars  $> 40$  (100%;  $n = 14$ ); carpels with the stalk 10–24 (17.7, 4.5, 14)  $\times$  1.5–2.7 (1.9, 0.36, 14) mm, the seed-bearing portion globose, 15–18 (16.5, 1.3, 14)  $\times$  14–19 (16.6, 1.4, 14) mm, smooth, rounded at apex, fruit wall  $< 1$  mm thick, deep red to black. Placentation ventral at maturity. Seed(s) 1 (or 2) per mature carpel, biconvex-lenticular, with circumferential groove, the aril scar lacking, the testa deep brown to black (often greenish when fresh), regular, smooth to finely pitted; rumination acicular, with needles occasionally slightly broadened.



DISTRIBUTION. New Guinea, and probably also the immediately adjacent islands (see MAP 3).

SELECTED SPECIMENS SEEN. **Indonesia.** IRIAN JAYA: Warsamsen R., 25 km E of Sorong, 60 m alt., *BW* 2980 (FR) (A, SING); Kebar Valley, Div. W. New Guinea, 450 m alt., *BW* 7193 (FR) (BO); Woda, Japen Is., Div. Geelvinkbaai, 50 m alt., *BW* 11207 (FR) (K), *BW* 11210 (FR) (A, SING). **Papua New Guinea.** WEST SEPIK PROVINCE: Aitape coastal area, coastal alt., *NGF* 524 (FR) (L, BRI). EAST SEPIK PROVINCE: Niksek Village, at April R. airstrip, middle April R., 4°42'S, 142°32'E, 50–150 m alt., *Rogstad* 814 (FL+fr), 832 (FL+fr), 833 (FL+FR) (all A, LAE, K); Sepik R. near Yellow R., *NGF* 3914 (fr) (A, NGF); [Malu region,] Sepik R. region, *Ledermann* 6814 (FR) (B, K); Sepik region, *Ledermann* 10409 (FL) (B, K, L); Koitaki, 460 m alt., *Carr* 12151 (FL) (SING). WESTERN HIGHLANDS PROVINCE: near Ruti E.L.G., Jimi Valley, Mt. Hagen, 450 m alt., *NGF* 38825 (FR) (A, BO, L, LAE). MOROBE PROVINCE: Aluki Village (12 km E of Lae), 60 m alt., *Rogstad* 782 (FL) (A, LAE, K); 7 mi N of Lae, near Butibum R., 65 m alt., *Hartley* 11863 (FR) (A, CANB); Gnalungumbum, 50 m alt., *NGF* 25576 (FL) (L, LAE). NORTHERN PROVINCE: Dobodura area, 125 m alt., *NGF* 2085 (FR) (L, LAE); between Divinikoari and Horata villages, 50 m alt., *Hoogland* 3529 (FR) (A, CANB, US); along Girua R., 1 km NW of Anonda airstrip, 60 m alt., *Hoogland* 3776 (FR) (A, CSIRO); Mayu Camp I, jct. of Ugat and Mayu rivers, Mt. Suckling, 305 m alt., *LAE* 56049 (FR) (A, K, L, LAE, US). CENTRAL PROVINCE: Mori R., Cape Rodney, Abau Subdistr., 65 m alt., *NGF* 38599 (FR) (A, L, LAE); Mori R., Abau Subdistr., 250 m alt., *NGF* 41840 (FL) (A, BO, L, LAE). WESTERN PROVINCE: Orovill Camp, Fly R., *Brass* 7411 (FR) (A, L). NEW BRITAIN: 7 mi SE of Benim Village, Wariai Subdistr., 300 m alt., *NGF* 27395 (FL) (L, LAE).

REGIONAL NAMES. "Adidionga," Orokaiva language (Mumuni), Northern Div., Papua New Guinea, *Hoogland* 3529. "Asiam," Biak language, Japen Is., Irian Jaya, *BW* 11210. "Atim," Bukawa language of the Suling clan, just NE of Lae, Papua New Guinea, *Rogstad* 782. "Fawss" or "pfahss," Niksek language, April R., Papua New Guinea, *Rogstad* 814. "Nimotiet," Kebar language, Div. W. New Guinea, Irian Jaya, *BW* 7193. "Oeloem," Mooi language, Warsamsen R., Irian Jaya, *BW* 2980. "Samoeben," Biak language, Japen Is., Irian Jaya, *BW* 11207.

LOCAL USE. The timber of *Polyalthia discolor* is used for house construction in the April River area (*Rogstad* 833), and for building houses and furniture in the Lae region (*Rogstad* 782).

ECOLOGY. The known altitudinal range is from 35 to 450 m above sea level. Of the 11 collections with details concerning habitat, eight were found on slopes and three at flat sites, but not on constantly inundated soils or those on which a thick root-humus mat had developed, or in peat swamps. This was confirmed by observations on members of a *Polyalthia discolor* population at April River (tributary to the Sepik), Papua New Guinea (*Rogstad*, in prep. a). Regeneration by seedlings, which was often pronounced, also exhibited this pattern.

Flowering begins when individuals reach the middle canopy but is generally prolific only when they achieve a place in the sun in the upper canopy. This species has the slowest-developing flowers of any species in the group, and individuals can have flowers reaching anthesis more or less continuously over periods of up to 1.5 months. Although the other species of the *P. hypoleuca* complex (except *P. ovalifolia*, for which no observations of pollinators have



yet been made) usually attract only one or two pollinators in any numbers, *P. discolor* flowers consistently drew several species of insects as potential pollinators. Pigeons and cassowaries have been observed eating the fruit (Pullen 8123).

The Annonaceae are generally known for their weak and somewhat flexible wood, a factor that may have contributed to the observation by Hoogland (3529, Northern Div., Papua New Guinea) that *Polyalthia discolor* was the "... most frequent standing tree in a patch of rainforest damaged by a cyclone."

COMMENTS. The type as designated by Diels, *Schlechter 18306*, was destroyed at Berlin, and I have been unable to locate any duplicates at A, B, BO, F, GH, K, KEP, L, MO, P, SAN, SAR, SING, U, or US. I have also been unable to find any collections of this species from the Ramu region of Papua New Guinea. Diels's description very clearly refers to the species recognized here. I have chosen as a neotype a collection that both matches the description by Diels and is representative of this group of specimens.

Identification of herbarium specimens of this species has caused much confusion due to their similarity in both flowers and fruits to *Polyalthia glauca*, also from the New Guinea region. This superficial resemblance caused Sinclair to comment (Carr 12151), "This is what Diels calls *discolor* but it is probably only a variety of *glauca*." However, as demonstrated in the morphometric analyses, *P. discolor* consistently has several unique features that distinguish it with a clarity commensurate with species status in this group, and thus I recognize it as such here.

Although *Polyalthia discolor* and *P. glauca* are very similar, the flowers of the former have more than 50 stamens (vs. less than 45 in *P. glauca*), more (vs. always fewer) than 27 carpels, and globose (vs. elongate) stigmas. These two species are much more difficult to distinguish in fruit, as is attested to by the fact that every herbarium specimen of *P. discolor* with fruit that I have seen has been misidentified as *P. glauca*. However, although the seed-bearing portions of the mature carpels are globose in both species, the fruit of *P. discolor* is generally larger than that of *P. glauca*. While the means for pedicel length and (distal) width and mature-carpel stalk length differ significantly ( $P < 0.05$ , unbalanced t-test,  $n = 14$  for *P. discolor*,  $n = 31$  for *P. glauca*) for the two species, there is enough overlap to cause confusion. However, specimens (other than immature ones of *P. discolor*) on the upper or lower ends of these scales can be identified. At any stage of development, the best means of separating fruits of these two New Guinean species is to count the scars left by the abscised stamens. Unfortunately, these are sometimes obscured by the expansion of the torus that accompanies fruit growth. Differences in stamen and carpel number and scars between these two species can be seen in FIGURE 20.

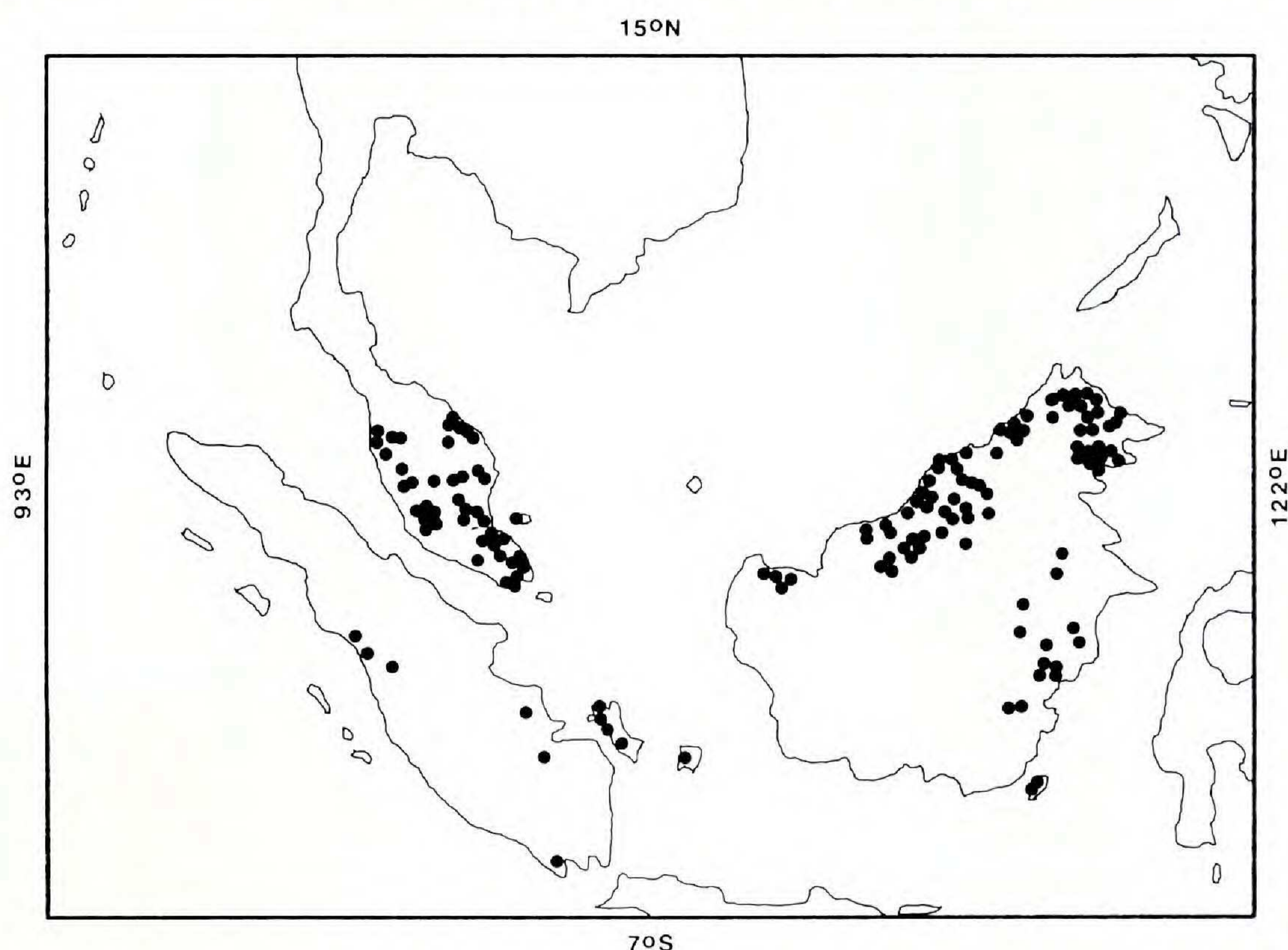
*Polyalthia discolor* and *P. glauca* are to date known to overlap geographically only in the middle Fly River region and possibly in north-central New Guinea (Rogstad, 1986), although with more comprehensive exploration, the area of overlap is likely to expand, especially since *P. glauca* has been found on Manus. Further study of the distribution and possible overlap of these species and comparative investigations of their autecologies are of critical importance to understanding the systematics and evolution of this group.



4. ***Polyalthia sumatrana*** (Miq.), Kurz, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 43: 53. 1874, *pro parte basionymica tantum*; *Guatteria sumatrana* Miq. Fl. Ned. Ind., Eerste Bijv. 380. 1861; *Monoon sumatranum* (Miq.) Miq. Ann. Mus. Bot. Lugduno-Batavum 2: 19. 1865. TYPE: [Sumatra,] Priaman, *Diepenhorst H.B. 2342* (lectotype, here selected, U: mature fruit and mature flower fragment). FIGURES 3B; 4A, D; 8B, D; 18A, B; 21C.

Tree to 24 m tall, DBH 4–25 cm; trunk rarely fluted at base; pneumatophores absent; bark white on younger trees and branches, remaining white to pale yellowish white on older trees; hoop marks not prominent on lower portion of bole; slash on larger trees revealing phloem rays reaching surface, phloem-ray apices 0.2–0.7 mm apart. Twigs with bark white to pale yellow-white, youngest growth glabrous (88%) or moderately tomentose (12%;  $n = 71$ ). Leaves with young petiole 3–12 (6, 1.5, 105) mm long, glabrous (80%) to moderately tomentose (20%;  $n = 71$ ) abaxially; lamina narrowly elliptic to elliptic, 9.2–28 (15.5, 3.2, 106)  $\times$  2.5–9.5 (4.5, 1.1, 106) cm, the apex acuminate to apiculate, 0.1–1.6 (0.9, 0.3, 106) cm long, the base rounded to acute, the secondary veins 19 to 80 (34.8, 10.2, 105) per side, not forming regular intramarginal vein; leaves when fresh flat with abaxial surface dull white (white mixed with gray or brown). Inflorescences in foliate axils, up to 4 per axil, and also borne on branches below leaves, tubercles lacking or poorly developed; peduncle extremely reduced, 0.6–2.5 (1.4, 0.4, 65) mm long, usually with only 1 terminal flower developing, lateral floral buds and developing flowers absent; bracts 1 to 3, oriented perpendicular to branch axis when only 1 flower per axil. Flowers with pedicel 7–25.4 (15.8, 5.4, 65) mm long, 0.6–1.8 (1.2, 0.3, 65) mm wide at base and 0.8–3 (1.9, 0.4, 65) mm at apex, glabrous (78%) to moderately pubescent (22%;  $n = 65$ ); pedicel bract sometimes present (43%;  $n = 65$ ), 4–8 mm above articulation. Sepals triangular, 0.7–3 (1.5, 0.48, 40) mm long, moderately (43%) to very densely (57%;  $n = 40$ ) tomentose abaxially, often caducous (38%;  $n = 65$ ) at floral maturity. Petals linear (97%) to basally clawed with obovate or flared distal portion (3%;  $n = 65$ ); outer petals 7.5–52 (28.4, 10.8, 65)  $\times$  1.5–6 (3, 0.8, 65) mm, the pubescence beginning adaxially on basal (11%), middle (49%), or distal (40%;  $n = 65$ )  $\frac{1}{3}$ , sparse throughout (62%), moderate throughout (11%), dense throughout (9%), or sparse throughout except abaxially at base where dense (18%;  $n = 65$ ), the midvein generally not visible abaxially; inner petals 9–56 (30.8, 11.4, 65)  $\times$  1.6–5.7 (2.9, 0.8, 65) mm; all petals turning yellow, or occasionally yellow-white (*S* 3020), yellow-brown (*S* 3057), maroon ([*SAN*] 3626), cream with pale pink tinge (*Sinclair et al.* 9313) or basal pink flush (*SAN* 21222), red (*SAN* 21459), or gray (*SAN* 56203) at maturity, “astringently fragrant” (*S* 38009; only this collection notes odor), tan to deep burgundy-red when dry. Torus 0.9–2.2 (1.4, 0.38, 62)  $\times$  1.3–4.4 (2.6, 0.67, 62) mm, gynoeceial portion concave (25%), flat (63%), or convex (12%;  $n = 65$ ). Androeceium 1.1–3.1 (2.7, 0.4, 65)  $\times$  3–6.2 (5, 0.75, 65) mm; stamens 80 to 232 (160.4, 33.6, 65), 0.8–1.7 (1.1, 0.15, 65)  $\times$  0.4–1.1 (0.78, 0.12, 65) mm. Gynoeceium 0.9–4.3 (2.2, 0.65, 65) mm across; carpels 5 to 49 (24.8, 8.8, 65), 0.8–2 (1.2, 0.22, 65) mm long, with small distal, abaxial patch of tomentum (65%) or moderately to densely tomentose (35%;  $n = 65$ ); stigmas globose (rarely slightly elongate), 0.2–0.8 (0.3, 0.1, 65) mm in diameter,





MAP 4. Distribution of *Polyalthia sumatrana*.

those of outermost ring not reflexed away from floral axis. Immature carpels firm, green with irregular red spots or streaks appearing 2–4 weeks before full maturity (such streaking diagnostic for this species within the *P. hypoleuca* complex), finally turning deep purple to black, the pericarp then soft and fleshy (juice laden) with sweet to bitter-sweet (pers. obs., Pasoh) or cinnamonlike (W. Kalimantan, *Schut K. 23*) taste or fragrant odor. Mature, dry fruits with pedicel 8–43 (21.7, 6.3, 107) mm long, 1.8–4.8 (3.2, 0.64, 106) mm wide at apex, glabrous (100%;  $n = 108$ ); stamen scars  $> 40$  (100%;  $n = 19$ ); carpels with the stalk 5–38 (15.1, 5.4, 105)  $\times$  1.3–4.4 (2.7, 0.64, 105) mm, the seed-bearing portion ellipsoid, 13–30 (22, 3.8, 106)  $\times$  9–19 (12.6, 2.3, 105) mm, sometimes longitudinally ridged (39%;  $n = 108$ ), tapered (89%) or blunt or rounded (11%;  $n = 108$ ) at apex; fruit wall  $> 1$  mm thick, burgundy to deep red-black. Placentation basal at maturity. Seed(s) 1 (or 2) per mature carpel, ellipsoid, with circumferential ridge, the aril scar present, the testa deep brown, finely to moderately pitted, not irregularly indented; rumination needles very fine.

**DISTRIBUTION.** From peninsular Malaysia to Sumatra, Borneo, and immediately adjacent islands (see MAP 4).

**SELECTED SPECIMENS SEEN.** **Malaysia.** PERAK: Chior F.R., Sungai Plus–Sungai Siput, 230 m alt., *FRI 5769* (FR) (KEP); sine loco, *Dr. King's collector (Lanit?) 6551* (FL) ( $\kappa$ ); Gunong Bubu, Ria Trong, 400 m alt., *FRI 11907* (FR) (KEP, L); Maxwell's Hill, 180 m alt., *SFN 38828* (FL) ( $\kappa$ , SING); Piah F.R., K. Kangsar, *Rahim Ismail KEPFN 99836* (FR) (KEP). TRENGGANU: Bukit Bauk F.R., 250 m alt., *FRI 2362* (FR) (KEP); near Geram Galong, Ulu Sungai, 65 m alt., *FRI 8357* (FR) (KEP); Ulu S. Trenggan, near K. Petang, Ulu



Trengganu, 275 m alt., *FRI 8438* (FR) (A, KEP); Sungai Loh, near K. Datok, 130 m alt., *FRI 10690* (FR) (A, KEP); Sekayu F.R., *FRI 11854* (FR) (KEP, L); along Sungai Pelong, *FRI 14885* (fl+FR) (A, KEP, SAR); Bukit Bauk VJR, Dungun, *FRI 25044* (FR) (KEP); Ulu Brang, 180 m alt., *SFN 33740* (FR) (A, KEP, SING); Jarangau S.L., Dungun Distr., *KEP 76674* (FR) (KEP). KELANTAN: Kuala Lebir Kechil, Sungai Lebir, *FRI 7075* (FR) (A, KEP, L); Sungai Lebir, 2 mi E of Kuala Aring, *FRI 7105* (FR) (KEP). SELANGOR AND KUALA LUMPUR FEDERAL DISTRICT: Gombak Reserve, *Murdock & Hashim 114* (FR) (KEP); Ulu Langat, Bukit Tangkol, K. Pansom, *KL 1360* (FR) (KEP), *KL 1375* (fl+FR) (A, KEP); Bukit Peringkat [Peningkot?], *KL 1494* (FR) (A, KEP); Sungai Buloh Reserve, [Abu] *CF Field No. 3335* (FL) (K, KEP); Ginting Simpoh, *Strugnell(?) [KEP?] 11225* (FR) (KEP); Gading F.R., Ulu Selangor, 370 m, *FRI 11229* (FR) (KEP, L); Ulu Gombak F.R., *Symington [KEP] 18162* (FR) (KEP); Bukit Lagong, *FRI 26595* (FR) (KEP); Sungai Buloh, *Walton [KEP] 29737* (FR) (KEP); Bukit Lajong F.R., 450 m alt., *Sow [KEP] 65141* (FR) (KEP); Ulu Gombak F.R., K.L. Distr., *KEP 94038* (FR) (A, KEP), *KEP 98269* (FR) (KEP), *KEP 99610* (FR) (A, KEP). PAHANG: Raub, Sungai Sempam, 920 m alt., *Soepadmo 725* (FL+fr) (KEP, KLU); Ulu Sungai Sepia, near Kuala Aur, *Shah & Noor 1904* (FR) (A, KEP, SING); Taman Negara, Bukit Terom, near K. Keniyum, 150 m alt., *FRI 8538* (FL) (KEP); Panching Forest, ca. 15 km N of Panching, Kuantan, 130 m alt., *Ogata [KEP?] 10432* (FR) (KEP); Raub, 365 m alt., *FRI 14689* (FL) (KEP); Bukit Saup, *Jaamat [KEP?] 16522* (FL) (KEP); Chini F.R., S of Tasek Chini, *FRI 17271* (FR) (KEP, L); Lesong F.R., 115 m alt., *FRI 19835* (FR) (A, KEP); Simpang Pertang, Ulu Tembeling, *SFN 22112* (FR) (A, KEP, SING); Lesong F.R., *FRI 23910*, *28028* (both FR) (both KEP); Aur F.R., K. Rompin, 50 m alt., *KEP 75883* (FR) (KEP); Krau Game Reserve, G. Benom, 300 m alt., *KEP 104427* (FR) (A, KEP). NEGRI SEMBILAN: Pasoh F.R., near Simpang Pertang, *Rogstad 508*, *509*, *527* (all FL) (all at A); Pasoh F.R., 50 m alt., *FRI 23496* (FR) (KEP). JOHORE: road to Sungai Kahang, N to Labis, *Shah & Sanusi 2107* (FR) (A, KEP, SING); path to Gunong Blumut, Kluang, 150 m alt., *Shah & Sanusi 2139* (FR) (A, KEP, SING); Tg. Sedili Kechil, E Johore coast, 30 m alt., *FRI 7688* (FL) (A, KEP); Ulu Endau, Labis F.R., *FRI 7869* (FL) (KEP, L), *FRI 7920* (FL) (KEP), *KEP 110402* (FL) (K, KEP); Kluang F.R., *FRI 8701* (FR) (A, KEP); NW Gunong Blumut, 548 m alt., *FRI 8820* (FR) (KEP, L); Labis F.R., *FRI 14783* (FL+FR) (A, KEP), *FRI 16073* (FR) (A, KEP); Gunong Pulai F.R., 335 m alt., *FRI 17639* (FR) (A, KEP); Tanjong Sedili Kechil, *SFN 28070* (FR) (KEP, SING); Sungai Kayu Ara, Mawai-Jemulang Road, *SFN 29330* (FR) (KEP, SING); Sungai Sedili, below Mawai, *SFN 36979* (FR) (A, KEP, SING); Bukit Mambai F.R., 50 m alt., *KEP 76295* (FL) (KEP, L); near Mersing F.R., 30 m alt., *KEP 77852* (FR) (KEP). SARAWAK: Gunong Mulu, Baram Distr., 550 m, [Anderson & Keng] *K 15* (FR) (A, SAR); Sabal Tapang, Ist Div., 130 m alt., *Stevens et al. 174* (FR) (A, SAR?); Gunong Api, Baram Distr., 500 m alt., *Chew Wee-lek 1106* (FR) (A), *1161* (FR) (A, L); Ulu Koyan, Mt. Dulit, IVth Div., 800–1000 m alt., *Richards (native collector) 1918* (FL) (A, K); near Kuching, *Haviland 2218* (FL) (K), *2694* (FL) (SAR); Lambir Hills F.R., Miri Distr., 300 m alt., *Dan bin Haji Bakar 3020* (FL) (A, SAR); upper Plieran, R. Kenaban, 560 m alt., *S 3501* (FR) (SAR, US); 10 km below Belaga, Kapit Distr., IIIrd Div., 500 m alt., *Jacobs 5201*, *5351* (both FL+FR) (both L, US); Ulu Pelagus, S. Iran, Kapit(?) Distr., 120 m alt., *Smythies 9469* (FL+fr) (K, SAR); Tatau, Ulu Anap, Sungai Takan, IVth Div., 215 m alt., *S 13763* (FL) (A, K, KEP, SAR); NE Lambir Hills, near Miri, 30 m alt., *S 16439* (FL) (A, SAR); Sabal F.R., Serian Distr., *S 16645* (FR) (A, L, SAR); S Sabal Tapang, Serian Distr., 50 m alt., *S 16990* (FR) (A, L, SAR); Rumah Temenggong, Begrih, Bawan, Balingian, 10 m alt., *S 19484* (FL+fr) (A, L, SAR); Pengiran/Chenaning divide, Ulu Mujong, Balleh, 600 m alt., *S 21161* (FR) (L, SAR); S Ukong, Miri, 10 m alt., *S 21403* (FL) (A, K, KEP, L, SAR); Kakus, Ulu Mayeng, *S 21705* (FL) (A, SAR); Bukit Dam, Ulu Dapoi, Marudi, IVth Div., *S 22955* (FR) (A, KEP, SAR); Long Dapoi, Tinjar, Marudi, IVth Div., 100 m alt., *S 22971* (FR) (A, KEP, SAR); Bok-Tisam, Bukit Mentagai, Marudi, IVth Div., 65 m alt., *S 23099* (FR) (A, SAR); Long Dam, Ulu Tinjar, Marudi, IVth Div., 115 m alt., *S 23373* (FR) (A, KEP, SAR); Ulu Dapoi, Long Kelaby, Tinjar, IVth Div., *S 23464* (FR) (A, KEP, SAR); Bukit Iju, Ulu Arip,



Balingian, IIIrd Div., 65 m alt., *S* 23623 (FR) (A, SAR); Ulu Sungei Bakong, Miri, 50 m alt., *S* 24409 (FR) (A, SAR); Lambir Natl. Park, Miri, *S* 25077 (FL) (SAR); Kapit, Balleh, Sg. Mengiong, IIIrd Div., *S* 29699 (FR) (SAR); Ulu Kakus, Anap, IVth Div., *S* 29974, *S* 29979 (both FR) (both A, KEP, SAR); Mata Kuching, Ulu Tinjar, S of Dulit Range, Baram Distr., *S* 34745 (FR) (KEP, SAR); Bukit Pendam, *SFN* 35735 (FR) (A, KEP, SING); Bukit Goram, Ulu Sg. Kapit, VIIth Div., 750 m alt., *S* 36184 (FR) (KEP, SAR); Nyabau F.R., Bintulu, IVth Div., *S* 37859 (FR) (KEP, SAR); Gunong Mulu Natl. Park, IVth Div., 430 m alt., *S* 38009 (FL+FR) (K, KEP, SAR), 425 m alt., *S* 38075 (FR) (KEP, SAR); Ulu Sungai Labau, Lambir Hills Natl. Park, IVth Div., 1210 m alt., *S* 38429 (FR) (KEP, SAR). SABAH: sine loco, *Agama*(?) 550 (FL) (A, PNH); Kinabatangan, *Puasa* 1069 (FR) (A, NY); Segaliud, Elopura, *Cuadra A* 1090 (FR) (A, K, KEP, SAN, US); Marutai, Tawau, 3 m alt., *Tandom BNBFD* 1786 (FL) (A, K); Sepilok F.R., *SAN A* 1969 (FR) (A, KEP, SAN); Table Estate, St. Lucia, Tawau, *Kadir A* 2103 (FL) (A, KEP, SAN); Gomantong, Elopura, Sandakan, 12 m alt., *Cuadra A* 2118 (FL) (A, K, KEP, SAN); Marutai, 8 m alt., *Maidin* 2428 (FR) (K); 7 m alt., *Maidin* 3057 (FL) (K); Bettotan [Bettotan?], 25 m alt., *Orolfo BNBFD* 3197 (FR) (A?, SAN), 30 mi WNW of Tawau, 30 m alt., *SAN A* 3698 (FR) (A, KEP, SAN); Bettotan, Sandakan, *Puasa BNBFD* 4544 (FL) (A, K, US); Apas Road, mi 7, 25 m alt., *Tandom BNBFD* 8806 (FR) (A, K); Sepilok F.R., Sandakan, 50 m alt., *Sinclair, Kadim, & Kapis* 9313 (FL) (A, K, SING); Beaufort Distr., 1 mi NE of Beaufort Township, 120 m alt., *SAN* 15052 (FL) (A, SAN); Kalabakan, 30 mi WNW of Tawau, 200 m alt., *SAN* 15263 (FR) (A, KEP, SAN); Sepilok F.R., Sandakan, 15 m alt., *SAN* 15488 (FL) (A, K, KEP, L, SAN); Kelumpang Balong, Tawau Distr., 80 m alt., *SAN* 17337 (FR) (SAN); Lalangot, ca. 1.5 mi from Pangkalan, Tawau, 40 m alt., *SAN* 18718 (FR) (A, KEP, SAN); Sepilok F.R., Sandakan, *SAN* 21222 (FL+FR) (K, KEP, SAN), *SAN* 21303 (FL) (A, KEP, SAN); Tawao, Elphinstone Prov., B.N.B. *Elmer* 20494 (FR) (A, US), 20877 (FL) (A, K, US), 21878 (FR) (A); Apas Road, mi 13, Tawau, *SAN* 21459 (FL) (K, KEP, SAN); Membalua F.R., Tawau Distr., *SAN* 22752 (FR) (A, KEP, SAN), *SAN* 22774 (FR) (KEP, SAN); Bukit Pasil, Lungmanis, Sandakan Distr., *SAN* 24238 (FR) (SAN); Lahad Datu Distr., Takun Kennedy Bay, 125 m alt., *SAN* 26065 (FL+FR) (SAN); W Sungai Strun, Tawau Distr., 150 m alt., *SAN* 26875 (FR) (SAN); Beaufort, Beaufort Distr., 30 m alt., *SAN* 28115 (FR) (SAN); Lohan, Ranau Distr., 1200 m alt., *SAN* 28758 (FR) (SAN); Mt. Andrassy, Tawau Distr., 300 m alt., *SAN* 29430 (FR) (SAN); Quoin Hill, Tawau Distr., 125 m alt., *SAN* 29464 (FR) (KEP, SAN); Ulu Sungai, Kalumpang, *SAN* 30480 (FL) (KEP, SAN); mi 15, Quoin Hill Road, Tawau, *SAN* 30616 (FL) (SAN), 35930 (FL) (K, SAN); Sepilok F.R., Sandakan, 15 m alt., *Brand [SAN]* 30983 (FL) (KEP, SAN); Bay Silabukan F.R., Lahad Datu Distr., 160 m alt., *SAN* 33432 (FR) (SAN); Halogilot, Beaufort Distr., 300 m alt., *SAN* 33754 (FR) (SAN); Sepilok F.R., Sandakan, 20 m alt., *SAN* 36709 (FL) (SAN); Lokan F.R., Segaliud, Sungai Munyed, Sandakan, 100 m alt., *Banang [SAN]* 36911 (FL) (KEP, SAN); Sepilok F.R., Sandakan, 30 m alt., *P. P. Sam [SAN]* 37540 (FL) (SAN); Labuk Road, mi 60, Sandakan Distr., *Meijer [SAN]* 37897 (FR) (SAN); Labuk Road trace, mi 81-82, Sandakan Distr., 150 m alt., *Meijer [SAN]* 38773 (FR) (K, SAN); Bettotan, Sandakan, *Puasa [SAN]* 38920 (KEP); Kabuk [Labuk?] Road, mi 60, Sandakan Distr., 40 m alt., *SAN* 39282 (FR) (SAN); Apas Road, mi 7, Tawau, *Tandom [SAN]* 44276 (FR) (KEP); Mt. Pock, Pagagau Road, Semporna Distr., 50 m alt., *Singh, Ahmad Talip, & Nordin [SAN]* 48900 (FL+FR) (SAN); Montinier Road, mi 12, Kg. Bambang, 300 m alt., *Madius [SAN]* 49259 (FL) (L, SAN); Ulu Sungei Kimanis, Papar Distr., 60 m alt., *Eging Banang [SAN]* 49353 (FL) (A, SAN); Elopura Distr., 20 m alt., *Puasa & Enggoh [SAN]* 55164 (FL) (KEP); Keningau, mi 8.5, Sook Plain, 350 m alt., *Ahmad Talip [SAN]* 55525 (FL) (A, SAN); Beaufort Hill, Beaufort Distr., *SAN* 66876 (FR) (L, SAN); Lumaku F.R., Mendalong, Sipitang Distr., *SAN* 72361 (fl+FR) (SAN); Telupid, Sandakan Distr., 100 m alt., *SAN* 75356 (FR) (L, SAN); Gunong Rara F.R., Kalabakan, 500 m alt., *SAN* 75659; Bengkoka F.R., Kudat Distr., 75 m alt., *SAN* 76076 (FL) (A, K, L, SAN); Ulu Sungei Dusun (NE of Sepilok), Sandakan Distr., 60 m alt., *SAN* 77357 (FR) (KEP, SAN); Crocker Range F.R., *SAN* 78305 (FR) (A, KEP, SAN); Ulu Segama, Tawau Distr., *SAN* 79179 (FR)



(KEP, SAN); Sepilok F.R., Sandakan Distr., *SAN* 83715 (FL+FR) (A, KEP, SAN); Bukit Tiulon, Nabawan, Keningau Distr., 350 m alt., *SAN* 841741 (FR) (KEP, SAN); Kuala Beatrice, Lahad Datu Distr., 270 m alt., *SAN* 84916 (FR) (K, KEP, SAN); Denum (Banum?), Ulu Sungai, Lahad Datu Distr., 425 m alt., *SAN* 85001 (FR) (KEP, SAN); Tawau Hill F.R., Tawau Distr., *SAN* 88228 (FR) (KEP, SAN); Mt. Tawai [Tawau?] F.R., Karamuak (Kuamut?), Sandakan Distr., 500 m alt., *SAN* 88722 (FR) (KEP, SAN); Sri Usukan, Tawau Distr., *SAN* 88974 (FR) (KEP, L, SAN); Lahad Datu Road, Sandakan Distr., 27 m alt., *SAN* 89169, *SAN* 89177 (both FR) (both KEP, SAN); Kg. Miruru, Mohd. Gan logging area, Ranau Distr., 600 m alt., *SAN* 90075 (FL) (A, SAN); Kalabakan, near Tawau, *SAN* 91500 (FL) (SAN). **Brunei:** R. Belait at K. Ingei, *BRUN* 187 (FR) (BRUN, KEP); Kuala Belalong, Temburong, 300 m alt., *BRUN* 465 (FL) (BRUN, KEP, L). **Singapore:** Sebtor [Seletar?], *Ridley* 6348 (FR) (A); Bukit Timah Reserve, *SFN* 35583 (FL) (A, KEP, SING). **Indonesia.** SUMATRA AND ADJACENT ISLANDS. Selatan: Rawas, Palembang, 200 m alt., *Dumas* 1630 (fl+FR) (BO, L); Muelok(?), Velve(?), 550 m alt., *Grashoff* 320 (FR) (BO, L); Marbau, Bilah, Bilah Pertama (Parbasir), *Toroës* 323 (FR) (A). Tengah: road from Kuala Belilas to Berapit R., Indragiri Uplands, 20 m alt., *Buwalda* 6669 (FL) (BO, L). Bangka: Lobok besar, 20 m alt., *Kostermans & Anta* 264 (FL) (A, BO, KEP); G. Manghol, 50 m alt., *Kostermans & Anta* 783 (FL) (A, BO, K); Lobok-besar, G. Pading, 20 m alt., *Kostermans & Anta* 942 (FL) (A, BO, K, L). KALIMANTAN: Kutei, R. Tiram, *Schut* K 23 (FR) (BO, K); Sambodja Village, Balikpapan, 60 m alt., *Schut* K 33 (FR) (A, BO); Poeloe Lauet, Soengei Paring, 100 m alt., *Verhoeff*(?) 80 (FR) (BO, L); Djaro Dam, ca. 10 km NE of Muara Uja, 100 m alt., *Vogel* 724, 784 (both FR) (both L); Kecamatan muara Ancalong, Long Lees, 100 m alt., *Wiriadinata* 1128 (FR) (A, BO); near Mt. Kemoel, W Koetai, 330 m alt., *Endert* 3684 (FL) (A, BO, K); Nunukan Is., 20 m alt., *Kostermans* 8629 (FR) (A, BO).

REGIONAL NAMES. "Antoi sembago" ("antoi" is applied to *Cyathocalyx* species in peninsular Malaysia), Indonesian?, Palembang, Sumatra, *Dumas* 1630. "Banetan puteh," language?, reported by Burkill (1966). "Banitan," language?, Lobok Besar, Bangka, *Kostermans & Anta* 264 and 942. "Binhud," Bandjar-Malay language, Balikpapan, Mentawir R., Kalimantan, *Sauveur* 99. "Binhut," Bandjar language, Balikpapan, Kalimantan, *Schut* K 33. "Buah sasak," Malay language(?), E. Kalimantan, *Wiriadinata* 1128. "Dada guan," Malay language(?), Pahang, peninsular Malaysia, *Jaamat* [KEP] 16522. "Delah," Iban language, Brunei, *BRUN* 897. "Delasai," Malay language, Brunei, *BRUN* 897. "Dilah," Iban language, Brunei *BRUN* 465. "Dilasai," Iban language, Kakus, Sarawak, *S* 21705. "Dilleh," Iban language, IVth Div., Sarawak, *S* 29979. "Kalamanjat," Tidong language, Marotai, Sabah, *Maidin* 3057. "Karai," Malay language, Bettotan, Sabah, *BNBFD* 3626; Kedayan and Sungei languages, Bettotan, Sabah, *BNBFD* 4544; dialect?, Kuching, Sarawak, *Zen* [S] 13022. "Karray," Kedayan language, Bettotan, Sabah, *BNBFD* 3197. "Kayu (or "pokok") dada bakok" (= wood or tree of the drug inducing stupor), Temuan language, Selangor, peninsular Malaysia, *KL* 690, *KL* 1360, and *KL* 1375. "Kerai" (also applied to other species of *Polyalthia* outside of the *P. hypoleuca* complex—e.g., *P. lateriflora*), Malay language, Sandakan region, Sabah, *SAN* A 1969. "Lirap (or sirap?)," Kutei language, R. Tiram, Kutei, Kalimantan, *Schut* K 23. "Medang bentawar," language?, reported by Burkill (1966). "Melada," language?, Pahang, peninsular Malaysia, *F. Gd.*(?) & *M. Soh*(?) [KEP] 15105. "Melian," language?, Selangor, peninsular Malaysia, *F. gd. Abu* CF Field No. 3335. "Melilin," Malay language(?), Selangor, peninsular Malaysia, *KEP* 99610; Johore, peninsular Malaysia, *Yeob*(?) 5873. "Mempisang," Malay language (a



general name referring to several species of Annonaceae), SE. Kelantan, *FRI* 7075; Johore, peninsular Malaysia, *KEP* 77852; Perak, peninsular Malaysia, *KEPFN* 29911. "Nyebulok," Kenyah language, Upper Baram R., Sarawak, *Chin See Chung* 2737. "Pahiding," Kayan language, Upper Plieran, Sarawak, *SAR* 3501. "Pisang-pisang" (pisang = banana), Malay language (a general name referring to several species of Annonaceae), Brunei, *Maidin* 3057; Pahang, peninsular Malaysia, *Hamid [KEP]* 10690; Tawau, Sabah, *SAN* 22752. "Pisang-pisang bukit," Malay language, Lahad Datu, Sabah, *SAN* 26065. "Purda hutan," Malay language, Kuala Belilas, Sumatra, *Buwalda* 6669. "Samukau," Iban language, IVth Div., Sarawak, *S* 13763. "Sarbah," Malay language, Upper Plieran, Sarawak, *SAR* 3501. "Selangan babi," Malay language, Tawau, Sabah, *Kadir A* 2106; Sandakan, Sabah, *A. Cuadra A* 2118. "Selaut," Melanau language, IVth Div., Sarawak, *S* 29974. "Selaut gunong," Malay language(?), Mt. Dulit, Sarawak, *Richards* 1918. "Selmu," language?, Lambir Hills, Sarawak, *Dan bin Haji Bakar* 3020. "Talooto," Sungei language, Elopura, Sabah, *A. Cuadra A* 1090. "Tingo," tidong language, Marutai, Sabah, *Maidin* 2428.

LOCAL USE. Trees of most species of Annonaceae have bark that can be removed in long strips, yielding excellent fiber. This is probably due to the anastomosing bast fibers of the phloem that continue into the bark. Several specimens of *Polyalthia sumatrana* (e.g., *Kostermans & Anta* 264 (Bangka), *Tandom BNB* 1786 (Sabah)) have notes indicating that the bark is often used as a source of fiber. The wood is used for roof timber in the Upper Plieran region of Sarawak and may deter insects (*Pickles SAR* 3501). Collections by Gadoh anak Umbai (*KL* 690, 1360, and 1375; peninsular Malaysia) are marked "poisonous" or "stupefying," and the local names, "kayu dada bakok" and "pokok dada bakok" can be loosely translated as "the tree of the drug that induces stupor." *KL* 1494 notes that the fruits are intoxicating, while *Chin See Chung* 2737 indicates that in the upper Baram River region of Sarawak, *P. sumatrana* is recognized as a good source for blowpipe wood.

ECOLOGY. This species has the highest and widest recorded altitudinal range of any in the *Polyalthia hypoleuca* complex, growing from near sea level to 1200 m alt. (*SAN* 28758 from Lohan, Ranau Distr., Sabah). It is found both on drier slopes and in flatter, more poorly drained sites, but apparently not in constantly inundated or peat-swamp habitats. Although occasional individuals are reported to achieve a height of 25 m, *P. sumatrana* rarely reaches the mid-canopy, being primarily a denizen of the lower understory.

The population of *Polyalthia sumatrana* at Pasoh F.R., peninsular Malaysia, puts out new vegetative growth synchronously twice per year but flowers irregularly, and sometimes periods greater than one year intervene between population flowerings. Only one report of floral fragrance exists for this species. However, since the flowers attract beetles thought to feed on rotting fruit, it is probable that they have some fragrance, perhaps one that resembles fermenting fruit, as has been found for other Annonaceae (Rogstad, in prep. b). Observations by M. and D. Leighton (pers. comm.) at Kutei National Park, Kalimantan, Indonesia, indicate that the flesh (not seeds) of mature fruits of *P. sumatrana* is eaten by numerous animals, including primates (*Pongo pyg-*



*moides*, *Hylobates muelleri*, *Macaca fascicularis*), squirrels (*Ratufa affinis*, *Callosciurus prevostii*, *C. notatus*), sun bears, hornbills (*Buceros rhinoceros*, *Ryticeros undulatus*, *R. corrugatus*, *Arthrococeros malayanus*, *Anorrhinus galeritus*), and other birds (*Calyptomena viridis*, *Calochomphus fuliginosis*, *Megalaima* sp., *Ducula aenea*, *Ptilinopus jambu*, and an unidentified bulbul). Hornbills have also been observed feeding on the fruits of *P. sumatrana* in Sabah, Malaysia (SAN 15263). The mature fruits of the members of the *P. hypoleuca* complex all have a similar taste and color to humans (pers. obs.), and thus each species may attract the wide array of frugivores (and seed dispersers?) observed for *P. sumatrana*.

COMMENTS. Miquel designated three syntypes: *Teysmann* 405 (sterile) and 4007 and *Diepenhorst* 2342. I have chosen the lectotype indicated above because it has diagnostic portions from mature fruit and a flower; a sheet at Kew previously placed with type materials for *Polyalthia sumatrana* (but for which no published reference has been found) bears portions of two Teysmann collections.

This species varies greatly, often on a local basis. For example, two petal forms have been collected from Bangka: the normal linear form (*Kostermans & Anta* 264), and one that is obovate or strongly flared distally (*Kostermans & Anta* 942). The latter shape has also been observed elsewhere (e.g., *Agama* 550, from Sabah). Research is needed to determine the degree to which flower-color variation is correlated with populations and geography and/or with differences in floral biology.

Leaf size provides another interesting example of local variability. In FIGURE 9 the three specimens of *Polyalthia sumatrana* with the largest leaves, as well as several of the smaller-leaved ones (e.g., *S* 16645), all come from Sarawak. The specimen with the largest leaves (*S* 29979) was collected quite near one exhibiting below-average leaf size (*S* 29974) at Ulu Kakus, Anap, IVth Division, Sarawak. Such variation is often observed at a single site and may be due to phenotypic variation.

Kochummen (1972) recognized *Polyalthia sumatrana* var. *macrocarpa*, based upon one specimen (*KEP* 104976; *KEP*) bearing relatively large fruits. When measurements from this specimen are included in the data set that generated FIGURE 15 and a PCA of this new data set is calculated, this specimen is indeed a very clear outlier (results not shown). However, it may be a mixed collection. The leaves have clearly been taken from some member of the *P. hypoleuca* complex. In contrast, the fruits, which are separate from the leaf-bearing branches, have very wrinkled, unridged mature carpels more like those of *P. clavigera* than the ellipsoid, prominently longitudinally ridged ones of *P. sumatrana*. Further, the seeds from *KEP* 104976 have a circumferential groove rather than a ridge and lack an aril scar; although the interior of the seeds has deteriorated somewhat, there are no rumination needles but rather a series of four rumination plates (in cross section) penetrating the endosperm. In addition, the gynoecial portion of the torus bears dense, minute tomentum, in contrast to the glabrous torus characterizing all the members of the *P. hypoleuca* complex. These seed and torus characters, like the external appear-



ance of the fruits, are more consistent with the fruits of the *P. clavigera*–*P. lateriflora* alliance of species (Rogstad, unpubl. data). Finally, there is only a single collection of this variety (even duplicates are apparently lacking), despite the fact that a few “typical” specimens of *P. sumatrana* have been collected from this region. This all suggests that the fruits from another species of Annonaceae have been mounted with vegetative material of one of the members of the *P. hypoleuca* complex.

*Polyalthia sumatrana* appears to grow in sympatry with *P. ovalifolia*, *P. glauca*, and *P. hypoleuca*. The leaves of *P. ovalifolia* are usually much larger and more broadly elliptic than those of *P. sumatrana*, and the two species differ in numerous floral and fruit characters as well. *Polyalthia sumatrana* differs from *P. glauca* in several easily detectable characters, including globose (vs. elongate) stigmas, usually many more than (vs. less than) 50 stamens, the ellipsoid (vs. globose) mature carpels, and circumferentially ridged (vs. grooved) seeds with an easily detectable (vs. undetectable) aril scar. It is less readily distinguished from *P. hypoleuca*, especially if one is examining a specimen of the former with only immature flowers. However, the pedicels of *P. hypoleuca* are usually much shorter (less than 9 mm in fruit) and have dense, short, rusty tomentum in both flower and fruit. If pedicels are not available, *P. hypoleuca* generally has smaller flowers with fewer stamens ( $< 45$ ) and carpels (usually  $< 10$ ).

5. ***Polyalthia hypoleuca*** Hooker f. & Thomson, Fl. Brit. India 1: 63. 1872, *pro parte florif.*, non *Guatteria hypoleuca* Miq. Fl. Ned. Ind., Eerste Bijv. Suppl. 381. 1861. TYPE: Singapore, [18]67, *Maingay 1516* (Kew Distr. 50) (lectotype, here selected, K, *pro parte*).

FIGURES 3A, B; 6A; 7A; 8D; 18D; 19C, D; 21B.

Tree to 50 m tall, DBH to 40 cm; trunk often fluted at base; pneumatophores absent; bark white to pale yellow, smooth on branches and trunk, with finely fissured or cracked patches appearing irregularly on bole; hoop marks not prominent on lower portions of bole; slash on larger trees revealing phloem rays reaching epidermis, phloem-ray apices 0.1–0.5 mm apart. Twigs with bark pale yellow-white, youngest growth glabrous (6%), or with moderate (39%) to dense (55%;  $n = 31$ ), short, rusty tomentum. Leaves with young petiole 3–7 (4.7, 1.2, 25) mm long, moderately (45%) to densely (55%;  $n = 31$ ) tomentose abaxially; lamina narrowly elliptic to elliptic, 6.1–12.5 (9, 1.6, 25)  $\times$  2–3.5 (2.6, 0.4, 25) cm, the apex acuminate to caudate, 0.6–1.4 (1.1, 0.2, 25) cm long, the base rounded to acute, the secondary veins 25 to 45 (32, 4.9, 25) per side, not forming regular weak intramarginal vein; leaves when fresh flat with abaxial surface dull white (tinged with brown, tan, or gray). Inflorescences in foliate axils, up to 4 per axil, and also borne on branches below leaves, tubercles absent or poorly developed; peduncle extremely reduced, 0.4–1.8 (0.9, 0.3, 26) mm long, usually with only 1 terminal flower developing, lateral floral buds and developing flowers absent; bracts 1 to 4, oriented perpendicular to branch axis when only 1 flower per axil. Flowers with pedicel 1–7.5 (2.7, 1.2, 26) mm long, 0.5–0.9 (0.7, 0.1, 26) mm wide at base and 0.5–1.2 (0.9, 0.4, 26) mm at

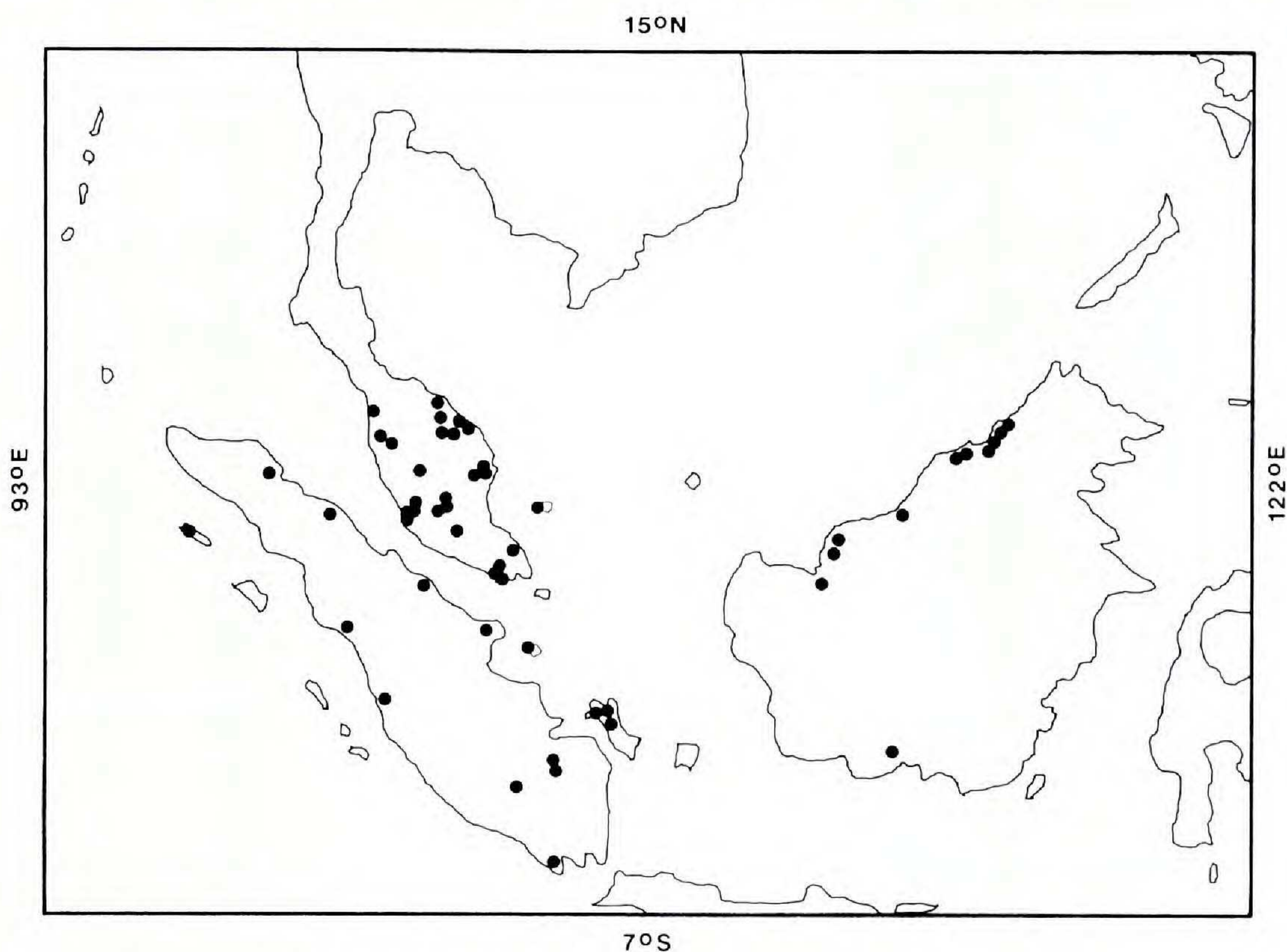


apex, with dense, rust-colored tomentum (100%;  $n = 26$ ); bract occasionally present (8%;  $n = 26$ ), 1–2 mm above articulation. Sepals triangular, 0.7–1.2 (1, 0.14, 16) mm long, very densely tomentose abaxially (100%,  $n = 16$ ), often (38%;  $n = 26$ ) caducous at floral maturity. Petals linear; outer petals 4–11 (7.1, 1.8, 26)  $\times$  1–2.4 (1.4, 0.4, 26) mm, the pubescence beginning adaxially on basal (42%), middle (54%), or distal (4%;  $n = 65$ )  $\frac{1}{3}$ , sparse to moderate throughout (58%), to sparse throughout except abaxially at base where dense (42%;  $n = 26$ ), the midvein not visible abaxially; inner petals 4–12 (7.5, 2.2, 26)  $\times$  0.8–1.9 (1.2, 0.3, 26) mm; all petals turning yellow at maturity, with perfumelike scent, deep burgundy-red when dry. Torus 0.3–0.8 (0.58, 0.12, 26)  $\times$  0.6–1.5 (1, 0.2, 26) mm, gynoeceial portion concave (7.7%), flat (57.7%), or convex (34.6%;  $n = 26$ ). Androeceium 0.7–1.8 (1.3, 0.3, 26)  $\times$  1.8–2.8 (2.3, 0.3, 26) mm; stamens 25 to 39 (32.3, 4, 26), 0.7–1.1 (0.8, 0.13, 26)  $\times$  0.5–0.8 (0.7, 0.07, 26) mm. Gynoeceium 0.5–1.5 (1, 0.23, 26) mm across; carpels 3 to 9 (5.4, 1.4, 26), 0.5–1.2 (0.9, 0.17, 26) mm long, glabrous (4%) or moderately to densely tomentose (96%;  $n = 26$ ); stigmas globose to moderately elongate, 0.2–0.7 (0.4, 0.16, 26) mm long, those of outermost ring not reflexed away from floral axis. Immature carpels green, slowly turning red 2–4 weeks before full maturity, finally deep purple to black, the pericarp then soft and fleshy (juice laden), with sweet or bitter-sweet taste. Mature, dry fruits with pedicel 4–9 (6.5, 1.4, 25) mm long, 1–2.3 (1.5, 0.4, 25) mm in diameter at apex, with dense, short, rusty tomentum (96%) or only moderately tomentose (4%;  $n = 25$ ); stamen scars  $< 40$  (100%;  $n = 21$ ); carpels with the stalk 2–5 (3.8, 0.9, 25)  $\times$  1.2–2.4 (1.5, 0.3, 25) mm, seed-bearing portion ellipsoid, 10–20 (15, 2, 25)  $\times$  9–14 (11, 1.1, 25) mm, not ridged, apex blunt or rounded (100%;  $n = 25$ ); fruit wall  $< 1$  mm thick, deep burgundy to black. Placentation basal at maturity. Seed 1 per mature carpel, ellipsoid, with circumferential ridge, the aril scar present, the testa deep brown, finely to moderately pitted, not irregularly indented; rumination needles very fine.

**DISTRIBUTION.** Peninsular Malaysia, Sumatra, Borneo, and immediately adjacent islands (see MAP 5).

**SELECTED SPECIMENS SEEN.** **Malaysia.** **KELANTAN:** Ulu Lebir Kechil, SE Kelantan, near Trengganu border, 370 m alt., *FRI 4413*, *FRI 4414* (both FR) (both KEP); Ulu Lebir F.R., *KEP 11695* (fl+FR) (KEP); G. Rabong, 610 m alt., *FRI 20623* (FL+FR) (A, K, KEP). **TRENGGANU:** Ulu S Trenggan, Kg. Melaka, 150 m alt., *FRI 10538* (fl+FR) (A, KEP); Bukit Bauk F.R., Dungun Distr., 25 m alt., *G. H. S. Wood 76094* (FR) (KEP). **PAHANG:** near Ulu Sungai Sepia, *Shah & Noor MS 2008* (FR) (A, KEP, SING); Lesong F.R., *FRI 25181* (FL) (KEP); Bukit Kajang F.R., Raub, *Jinal [KEP] 20351* (FR) (KEP); Pelican Road, T. Lapah Tempwiang, Kuantan-Pahang, *Jaamat & Sow [KEP] 43190* (FR) (KEP). **SELANGOR AND KUALA LUMPUR FEDERAL DISTRICT:** Telok F.R., *Rogstad 934*, *947* (both FL) (both A); Bangi, *Balgooy 2199* (fl+fr) (KEP, L); Telok F.R., near Klang, *Hamid & Yeop (Yeob?) [KEP] 3267* (fl) (KEP); Bukit Changgang, Klang, *SFN 33955* (FR) (A, KEP, SING); near Kuala Lumpur, *Sudin [KEP] 41882* (FL+FR) (KEP); Telok F.R., Klang, *KEP 45808* (FR) (KEP). **NEGRI SEMBILAN:** Pasoh F.R., near Simpang Pertang, *Rogstad 912*, *933*, *942* (all FL) (all A); Tampin F.R., 540 m alt., *FRI 14216* (FR) (KEP); Gunong Angsi F.R., 400 m alt., *FRI 14631* (FL) (A, KEP). **JOHORE:** Segamat Wildlife Reserve, *FRI 17148* (fl+FR) (A, KEP); Sungai Kayu, *SFN 32189* (FR) (A, KEP, SING); Pengkalan Raja, Pontian, *SFN 36644* (fl+FR), *SFN 36697* (FL+FR) (both A, KEP, SING). **SARAWAK:** Buglgan(?), Tj.



MAP 5. Distribution of *Polyalthia hypoleuca*.

Kelepis(?), *S* 690 (FR) (KEP, SAR); S Entulang, Simanggang, *S* 13120 (FR) (SAR). SABAH: Kumanis F.R., Papar Distr., 3 m alt., *SAN A* 4600 (FR) (KEP, L, SAN); K. Klias Saratok, Beaufort Distr., *SAN* 27307 (FR) (KEP, SAN, SAR); Melaliah N.F. Reserve, Sipitang Distr., 15 m alt., *SAN* 27953 (FR) (KEP, L, SAN); Seratok Camp, Beaufort Distr., 10 m alt., *SAN* 35236 (FL) (K, SAN); along rail line Lumat, Beaufort Distr., *Binideh* [*SAN*] 58445 (FR) (SAN). **Brunei:** Seria peat swamp, 8 m alt., *S* 5892 (fl) (BRUN, FRI); Badas swamps, *Sinclair & Kadim* 10460 (fr) (A, SING); Kuala Belait, Badas State Land, 7 m alt., *SAN* 17457 (FL) (A, KEP, L, SAN). **Singapore:** Jurong Road, *SFN* 26163 (FL+fr) (A, FRI, SING). **Indonesia.** SUMATRA AND ADJACENT ISLANDS: Riouw en Ond., Koeantan Distr., Sei Rambei [Sumatra?], 70 m alt., *bb* 23472 (FR) (A, BO, L). Utara: Masihi F.R., Asahan, E coast, *Krukoff* 4095 (FR) (A, L, US). Tengah: Bengkalis, Sekoedi [E coast], 5 m alt., *bb* 21285 (fl) (A, BO, L); Pulau Gelang, 4 m alt., *bb* 29166 (fl+FR) (A, BO, L). Selatan: Palembang, 15 m alt., *Zwan WF(?)* 1172 (FR+fl) (BO, L); Belimbing, 6 m alt., *bb* 28536 (FL) (A, BO, K). Bangka: Lobok-besar, 20 m alt., *Kostermans & Anta* 148 (FL+FR) (A, BO, KEP?), 199 (fl+FR) (A, BO), 1072 (FL+FR) (A, BO, LAE), 1171 (FR) (A, BO, K, KEP). KALIMANTAN: near Sampit, 5 m alt., *Kostermans* 8134 (FL) (A, BO, L).

REGIONAL NAMES. "Ban aan aandoel," Indonesian?, Palembang, Sumatra, *Zwan* 1172. "Banittan," Indonesian?, Sumatra, *L. B.* 72. "Kayu selaut," Malay language? (kayu = wood, laut = sea), Sarawak, *S* 690. "Mahawai," language?, Sampit, S. Kalimantan, *Kostermans* 8134. "Manitan," language?, Pahang, peninsular Malaysia, *KEP* 78666. "Melian," language? (in Burkill, 1966). "Melinin," language? (in Burkill, 1966). "Mempisang," Malay language (a general name for several species of Annonaceae), Kelantan, peninsular Malaysia, *KEP* 11695. "Pisang-pisang," Malay language (pisang = banana) (a general name for several species of Annonaceae), Pahang, peninsular Malaysia, *Jinal* [*KEP*]



20351; Papar Distr., Sabah SAN A 4600. "Ridis," language?, Lobok Besar, Bangka, *Kostermans & Anta* 1072. "Selaut," Iban language?, Simanggang, S. Sarawak, *S* 13120. "Telinga basing," language?, Beaufort Distr., Sabah, SAN 27307. "Usai," language?, Lobok Besar, Bangka, *Kostermans & Anta* 148.

LOCAL USE. As in many Annonaceae, the bast fibers of the phloem and bark anastomose to yield a bark that can be removed in strips and makes excellent rope or fiber. This quality is noted by J. A. R. Anderson (*S* 690), who indicated that the natives of southern Sarawak use the bark of *Polyalthia hypoleuca* to make string and the wood to make bows. Burkill (1966) noted that this fiber withstands sea water. The wood of larger *P. hypoleuca* trees may also be used for crate and toy construction in peninsular Malaysia (Timber Utilization Chart, Forest Research Institute, Kepong, Selangor, Malaysia). In addition, Burkill (1966) reported that a decoction of the roots of this species is given after childbirth in peninsular Malaysia.

ECOLOGY. Altitudinal range is recorded as from near sea level to 610 m alt. Although Sinclair (1955) indicated that *Polyalthia hypoleuca* attains a height of 15 m, I have observed several individuals at Pasoh F.R., peninsular Malaysia, that have grown to over 30 m; flowering is generally most pronounced in tall individuals with exposed crowns. At Pasoh this species is restricted to drier slopes and does not appear to grow at seasonally or constantly inundated sites with little or no peat development. It is somewhat puzzling, therefore, that it (or a cryptic sibling species?) does grow in peat-swamp forests, but only where a thick peat mat has developed; *P. hypoleuca* is unable to grow in inundated bare clay soils. Possible reasons for this will be suggested in a subsequent article (Rogstad, in prep. a).

Ten distinct waves of flowering of varying intensity divided into two main periods were observed at Pasoh over the period of a year. Each main period was immediately preceded by the initiation of a flush of vegetative growth. The waves are very synchronized among the members of the population. Pollination appears to be effected, in both the Pasoh and Telok populations, primarily by the same species of beetle.

COMMENTS. Unfortunately, the type designated by Hooker and Thomson (1872) is a mixed specimen consisting of flowering and fruiting branches of *Polyalthia hypoleuca* and fruiting ones of *P. sumatrana*. Sinclair (1955) noted this mixed specimen, and here I lectotypify *P. hypoleuca* based on it.

*Polyalthia hypoleuca* grows in sympatry with *P. glauca*, *P. ovalifolia*, and *P. sumatrana*. Characters separating *P. hypoleuca* from *P. sumatrana* are included in the comments under the latter species. It can be distinguished from *P. glauca* and *P. ovalifolia* because the latter two species have elongate, clavate stigmas more than 64 percent of the length of the carpels, stigmas of the outermost ring bent outward at an angle greater than 30°, short (usually less than 10 mm) pedicels in fruit, and seed-bearing portions of the carpels globose at maturity.

Due to a very close morphological resemblance, *Polyalthia hypoleuca* is the species most likely to be confused with *P. multinervis*. As indicated in the PCA analyses of characters (e.g., see FIGURE 17), *P. multinervis* does differ slightly



from *P. hypoleuca*: it has slightly larger flowers, glabrous or very sparsely pubescent (vs. densely tomentose) pedicels, and mature carpels acute to acuminate (rather than blunt) at the apex. These two species also differ in floral biology. Populations of *P. hypoleuca* studied in peninsular Malaysia had very fragrant flowers from the time of stigma receptivity until the petals abscised at anther dehiscence. Flowers at the equivalent stage from numerous individuals of *P. multinervis* studied at April River, Papua New Guinea, lacked detectable fragrance. The main pollinator of *P. hypoleuca* in peninsular Malaysia is of a strikingly different morphology than the main pollinator of *P. multinervis* in Papua New Guinea (Rogstad, in prep. b). *Polyalthia hypoleuca* has not been collected east of Borneo, while *P. multinervis* is thus far known only from the April River region of the Sepik River drainage in Papua New Guinea.

The sum of the evidence at hand indicates that slight but constant morphological differences exist between these two entities, that biological differences exist between them such that if they were to grow sympatrically, gene exchange might well not occur, and that they are geographically isolated. The two entities thus appear to conform to the evolutionary species concept defined above, and I therefore recognize them as such here.

6. ***Polyalthia multinervis*** Diels, Bot. Jahrb. Syst. **52**: 178. 1915. TYPE: [Papua New Guinea,] Sepik River region, April River, Sept. 1912, *Ledermann* 8835 (fl) (holotype, B; isotypes, K, SING).

FIGURES 3D; 4E; 8A; 19A, B; 21D.

Tree to 30 m tall, DBH to 30 cm; trunk often fluted at base; pneumatophores absent; bark white to pale yellow, smooth on branches and trunk, with finely fissured or cracked patches appearing irregularly on bole; hoop marks not prominent on lower portions of bole; slash on larger trees revealing phloem rays reaching epidermis, phloem-ray apices 0.1–0.5 mm apart. Twigs with bark pale yellow-white, youngest growth glabrous (18%) or with moderate short, rusty tomentum (82%;  $n = 11$ ). Leaves with young petiole 4–5 (4.6, 0.5, 8) mm long, glabrous (9%) to moderately tomentose (91%;  $n = 11$ ) abaxially; lamina narrowly elliptic to elliptic, 8.4–10.6 (9.4, 0.7, 8)  $\times$  2.3–3.4 (2.8, 0.4, 8) cm, the apex acuminate to caudate, 0.5–1.1 (0.8, 0.2, 8) cm, the base rounded to acute, the secondary veins 16 to 29 (25, 4.1, 8) per side, not forming regular weak intramarginal vein; leaves when fresh flat with abaxial surface dull white (tinged with brown, tan, or gray). Inflorescences in foliate axils, up to 4 per axil, or borne on branches below leaves, tubercles absent or poorly developed; peduncle extremely reduced, 0.4–1.4 (0.8, 0.3, 8) mm long, usually with only 1 terminal flower developing, lateral floral buds and developing flowers absent; bract(s) 1 to 4, oriented perpendicular to branch axis when only 1 flower per axil. Flowers with pedicel 2–7 mm long, 0.6–1 mm wide at base and 0.9–1.2 mm at apex, glabrous or rarely with very sparse pubescence; bract always absent. Sepals triangular, 1–1.2 mm long, very densely tomentose abaxially, often caducous at floral maturity. Petals linear (100%,  $n = 18$ ); outer petals 7–12  $\times$  1.3–2.1 mm, the pubescence always beginning adaxially on basal  $\frac{1}{3}$ , sparse to moderate throughout, the midvein not visible abaxially; inner petals



6.6–13 × 1.3–2 mm; all petals turning yellow at maturity, detectable fragrance absent, deep burgundy-red when dry. Torus 0.5–1.1 × 0.9–1.1 mm, gynoecial portion convex. Androecium 1.3–2.4 × 2.5–3.2 mm; stamens 26 to 32, 0.9–1.2 × 0.8–1 mm. Gynoecium 0.7–1 mm across; carpels 2 to 7, 1.1–1.3 mm long, moderately to densely tomentose; stigmas globose to moderately elongate, 0.3–0.6 mm long, those of outermost ring not reflexed away from floral axis. Immature carpels slowly turning red 2–4 weeks before maturity, finally deep purple to black, with soft, fleshy (juice-laden) pericarp tasting sweet or bitter-sweet. Mature, dry fruits with pedicel 6–10 mm long, 1.2–1.9 mm in diameter at apex, glabrous or with very sparse, short pubescence; stamen scars < 40; carpels with stalk 2–5 × 1.4–1.9 mm, seed-bearing portion ellipsoid, 18–22 × 7–12 mm, not ridged, acutely tapering at apex; fruit wall < 1 mm thick, burgundy to black. Placentation basal at maturity. Seed 1 per mature carpel, ellipsoid, with circumferential ridge, the aril scar present, the testa deep brown, finely to moderately pitted, not irregularly indented; rumination needles very fine.

DISTRIBUTION. Sepik River basin of Papua New Guinea in middle to lower April River region (see MAP 3).

SELECTED SPECIMENS SEEN. **Papua New Guinea.** EAST SEPIK PROVINCE: Niksek Village, April River airstrip, middle April R. (tributary to Sepik R.), 4°42'S, 142°32'E, 50–150 m alt., *Rogstad* 813 (FL+fr), 817, 818, 819 (all FL), 820 (FL+FR), 828 (FL+fr), 829 (FL+FR) (all A, LAE); [April R. region, Sepik Valley, ca. 15–20 km upriver from Ambunti,] *Ledermann* 8835 (fl) (B, K, SING).

REGIONAL NAMES. “Fawss” or “pfahss,” Niksek language, April R., Papua New Guinea (*Rogstad* 829).

LOCAL USE. Timber of this species is used for house construction in the April River region of Papua New Guinea (*Rogstad* 829).

ECOLOGY. *Polyalthia multinervis* is thus far known only from 80 to 200 m alt. since it has only been collected from the April River region. More information on all aspects of this species is obviously needed. In the forests around Niksek Village (April River airstrip), flowering individuals are generally small to medium-size trees. However, their crowns are at or near canopy level because they grow almost exclusively in somewhat stunted forest on a thick, “peaty” humus mat (mat depth may exceed 1 m) that develops mostly in flatter areas and yields black water drainage. Areas with this root-humus mat are not true peat swamps; they are well drained and are not even intermittently inundated. Tracts on which the mat develops may be ecologically similar to the closed kerangas (heath) forests of Sarawak described by Brunig (1974), but this can only be determined by comparative investigations. *Polyalthia multinervis* appears to be a late secondary species, not growing in the full sun of open gaps but also not regenerating in the deepest forest. The most prolific regeneration can be found on well-developed root mats on banks well above the April River. As in *P. hypoleuca*, flowering in this species appears to occur in several distinct waves each year. Although mature individuals vary in the number of waves in which they flower, flowering of all plants within a wave is highly synchronized (see also *P. hypoleuca*, and *Rogstad*, in prep. b).



COMMENTS. Diels (1915) was apparently not familiar with *Polyalthia hypoleuca* since he made no mention of its similarity to *P. multinervis*. Despite this close resemblance, I have maintained the two as distinct species (see comments under *P. hypoleuca*). The New Guinea region is very poorly collected, and thus this classification scheme may require review as more information accumulates.

The type material designated by Diels (1915) that I have seen bears only immature flowers. However, enough characters are present to distinguish this entity clearly from *Polyalthia discolor* and to confirm its identity with specimens I have collected in the April River region. Diels also mentioned the only other collection of this species previous to mine, *Ledermann 9843*, stating that it bore fruit. I have been able to locate but one fruiting sheet of this collection (at L), and it bears only an apparently mature fruit pedicel with the developed carpels missing. The stamen scars number less than 50, and the pedicel agrees with *P. multinervis* as found at April River.

### Uncertain Taxa

The possibility that a putative variety of *Polyalthia sumatrana*, var. *macrocarpa*, may be based on a mixed collection has been discussed above under that species.

Two specimens from the Andulau Forest Reserve, Kuala Belait District, Brunei (*Sinclair & Kadim 10454*, *SAN 17486*), and one from R. Belait at K. Ingei, Brunei (*BRUN 187*), are most closely allied, on the basis of flower and fruit characters, with *Polyalthia sumatrana*. However, they differ in their pedicels that are moderately tomentose and are occasionally fully articulated about 8–11 mm above the articulation here interpreted as separating the peduncle from the pedicel. The latter character is variable, however, even on a single specimen. Since “typical” specimens of *P. sumatrana* can also be found in this region (e.g., *BRUN 465*, *BRUN 897*), and since no population has been found that exhibits constant and discrete variation in these characters (as has been seen in *P. ovalifolia*, for example), I have not recognized this variation formally.

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**APPENDIX 1. Specimens examined for leaf papillae\*  
and for seeds with spiniform endosperm ruminations.†**

- Anaxagorea javanica* Blume var. *tripetala* Corner: *Elmer* 21131 (A).
- A. luzonensis* Gray: *Ramos BS* 13623 (A).
- A. petiolata* R. E. Fries: *A. C. Smith* 3192 (MO).
- A. phaeocarpa* Martius: *Anderson* 12139 (MO).
- A. rufa* Timmerman: *Gentry & Tillett* 10883 (MO).
- A. sylvatica* R. E. Fries: *Mexia* 5053 (MO).
- Annona muricata* L. and *A. squamosa* L.: specimens from living collections at Fairchild Tropical Garden, Coral Gables, Florida.
- Artabotrys harmandii* Finet & Gagnep.: *Pierre* 423 (A).
- A. siamensis* Miq.: *Rogstad* 959; *Sargent s.n.*, 16 Oct. 1903 (MO).
- A. suaveolens* Blume: *Maxwell* 81-206 (MO); *Rogstad* 831.
- A. trichopetalus* Merr.: *Elmer* 20489 (A).
- A. zeylanicus* Hooker f. & Thomson: *Saldanha* 16365 (A); *Waas* 934 (A).
- Asimina triloba* (L.) Dunal: specimen in living collection at Arnold Arboretum, Jamaica Plain, Massachusetts.
- Bocageopsis canescens* (Spruce) R. E. Fries: *Prance et al.* 5929, 8792 (both MO).
- B. mattogrossensis* (R. E. Fries) R. E. Fries: *Maas et al.* 6242 (MO).
- B. multiflora* (Martius) R. E. Fries: *Prance et al.* 22714, 25798 (both MO); *Silva & Rosario* 5849 (A).
- Cleistochlamys kirkii* (Bentham) Oliver: *Pereira & Correia* 2351 (MO); *De Carvalho* 1045 (MO).
- Cleistopholis glauca* Pierre ex Engler & Diels: *Leeuwenberg* 6467 (MO); *Louis* 12459, 12563 (both MO).
- C. patens* (Bentham) Engler & Diels: *Darko* 732 (MO); *Louis* 7993 (MO).
- C. staudtii* Engler & Diels: *Bates* 1568 (MO).
- Crematosperma anomalum* R. E. Fries: *Correa & Dressler* 887, 1060 (both MO); *Stern et al.* 107 (A).
- C. cauliflorum* R. E. Fries: *Bristan* 1341 (MO); *Diaz & Jaramillo* 1229 (MO); *Lleras et al.* 16879 (MO).
- C. macrocarpum* Maas: *Liesner & González* 9763 (MO).
- C. pedunculatum* (Diels) R. E. Fries: *Klug* 3726 (A).
- Desmos cochinchinensis* Lour. and *D. dasymaschalus* (Blume) Safford: specimens in living collections at Kebun Raya, Bogor, Indonesia.
- Enantia chlorantha* Oliver: *Bates* 1959 (MO); *Leeuwenberg* 7355 (MO); *Zenker* 441 (MO).
- E. polycarpa* (DC.) Engler & Diels: *Baldwin* 10696 (MO).

\*See also APPENDIX 2.

†For most species several specimens have been examined, but usually only one representative collection is noted. *Rogstad* collections are deposited at A.



- Ephedranthus amazonicus* R. E. Fries: *Prance et al.* 11555, 18787 (both MO).  
*E. guianensis* R. E. Fries: *Gentry et al.* 29075 (MO).  
*E. pisocarpus* R. E. Fries: *Schatz et al.* 732 (MO).  
*Goniothalamus giganteus* Hooker f. & Thomson: *Rogstad* 985.  
*G. tortilipetalus* Henderson: *Rogstad* 566.  
*Lettowianthus stellatus* Diels: *Seuisei* S1027 (MO).  
*Malmea depressa* (Baillon) R. E. Fries: *Croat* 24646 (MO); *Lundell* 4852 (MO).  
*M. obovata* R. E. Fries: *Riedel s.n.* (A).  
*Meiocarpidium lepidotum* Engler & Diels: *De Wilde* 1942 A, 2735 (both MO); *Zenker* 3602 (MO).  
*Melodorum fruticosum* Lour.: *Scortechini* 1946 (SING).  
*Monocarpia marginalis* (Scheffer) James Sincl.: *De Vogel* 4492 (MO).  
*Monodora myristica* Dunal: specimen growing at the Forest Research Institute, Kepong, Selangor, Malaysia.  
*Oncodostigma monosperma* (Hooker f. & Thomson) James Sincl.: *Rogstad* 920.  
*Oncodostigma* sp.: *Rogstad* 957.  
*Onychopetalum krukoffii* R. E. Fries: *Krukoff* 5326 (MO).  
*O. lanceolatum* R. E. Fries: *Krukoff* 6909 (MO).  
*O. lucidum* R. E. Fries: *Krukoff* 8214 (MO).  
*Oxandra acuminata* Diels: *Croat* 19729 (MO).  
*O. asbeckii* (Pulle) R. E. Fries: *Mori & Boom* 15170 (MO).  
*O. eneura* Diels: *Croat* 18738 (MO).  
*O. espintana* (Spruce) Baillon: *Gentry, Aronson, & Ramírez* 26744 (MO).  
*O. laurifolia* Rich.: *Duss* 4180 (MO).  
*O. leucodermis* (Spruce) Warm.: *Liesner* 6983 (MO); *Liesner & Clark* 8949 (MO).  
*O. longipetala* R. E. Fries: *Holdridge* 6313 (MO).  
*O. xylopioides* Diels: *Huashikat* 1257 (MO).  
*Phaeanthus* sp.: *Rogstad* 938.  
*Piptostigma fasciculata* (Wilde) Boutique: *Germain* 2396 (MO); *Toussaint* 2151 (MO).  
*P. glabrescens* Oliver: *Thomas* 510 (MO).  
*P. pilosum* Oliver: *Thomas* 4726, 4755 (both MO).  
*Platymitra siamensis* Craib: *Rogstad* 796.  
*Polyalthia angustissima* Ridley: specimen in living collections at Singapore Botanical Garden.  
*P. brunneifolia* James Sincl.: *James Sinclair* 24179 (A).  
*P. bullata* King: *FRI* 11643 (KEP).  
*P. capuronii* Cavaco & Keraudren: *Capuron SF* 11795 (P).  
*P. cf. cauliflora* Hooker f. & Thomson: *Rogstad* 997.  
*P. cinnamomea* Hooker f. & Thomson: *Rogstad* 936.  
*P. clavigera* King: *Curtis* 2444 (SING).  
*P. discolor* Diels: *Rogstad* 814, 832.  
*P. emarginata* Diels: *Capuron* 20977-SF (P).  
*P. gigantifolia* Merr.: *Ramos & Edaño* 36966 (SING).  
*P. glauca* (Hassk.) Mueller: *Rogstad* 939, 944, 945, 966.  
*P. gracilis* Burck: *Versteeg* 1408 (BO).  
*P. heteropetala* Diels: *Ghesquier* 4942 (P).  
*P. hypoleuca* Hooker f. & Thomson: *Rogstad* 912, 916, 942.  
*P. jenkinsii* (Hooker f. & Thomson) Hooker f. & Thomson: *Rogstad* 968.  
*P. lateriflora* (Blume) King: *Rogstad* 931.  
*P. longifolia* (Sonn.) Thwaites: *Rogstad* 960.  
*P. macropoda* King: *Kostermans* 7360 (SING).  
*P. michaelii* C. T. White: *NGF* 77111 (LAE).  
*P. multinervis* Diels: *Rogstad* 813, 817–819, 829.  
*P. obliqua* Hooker f. & Thomson: *Rogstad* 935.



- P. oblongifolia* Burck: *Ramos* 1595 (A).  
*P. oligosperma* (Danguy) Diels: *Thouvenot* 62 (P).  
*P. oliveri* Engler & Diels: *Baldwin* 10394 (MO); *Enti* 1701 (MO); *Oldeman* 856 (MO).  
*P. ovalifolia* Rogstad: *Buwalda* 7797 (A).  
*P. pedicellata* A. C. Smith: *A. C. Smith* 647 (BO).  
*P. rumphii* (Blume) Merr.: *Rogstad* 922.  
*P. sclerophylla* Hooker f. & Thomson: *Rogstad* 930.  
*P. stenopetala* (Hooker f. & Thomson) Ridley: *Dev* 165 (KLU).  
*P. stuhlmannii* (Engler) Verdc.: *Harris* 3635 (MO).  
*P. suaveolens* Engler & Diels: *Gilbert* 8500 (MO); *Leeuwenberg* 5082, 7322 (both MO).  
*P. suberosa* (Roxb.) Thwaites: specimens from living collections at Fairchild Tropical Garden, Coral Gables, Florida.  
*P. sumatrana* (Miq.) Kurz: *Rogstad* 508, 509, 527.  
*P. thorelii* Finet & Gagnep.: *Pierre* 1506 (SING).  
*Polyalthia* sp.: *Rogstad* 987.  
*Polyceratocarpus gossweileri* (Exell) Paiva: *Breyne* 752 (MO).  
*P. microtrichus* (Engler & Diels) Ghesq. ex Pellegrin: *Zenker* 478 (MO).  
*P. parviflorus* (Engler & Diels) Ghesq.: *Bos* 6684 (MO); *Jacques-Georges* 16832 (MO).  
*Pseudephedranthus fragrans* (R. E. Fries) Aristeg.: *Maguire et al.* 60189 (MO).  
*Pseudoxandra coriacea* R. E. Fries: *Prance, Steward, Ramos, & Pinheiro* 11468 (MO).  
*P. cuspidata* Maas: *C. C. Berg et al.* 757 (MO); *Prance & Sylva* 58673 (MO).  
*P. guianensis* R. E. Fries: *A. C. Smith* 2665 (MO).  
*P. lucida* R. E. Fries: *Steyermark & Delascio* 129373 (MO).  
*P. polyphleba* (Diels) R. E. Fries: *Gentry, Vasquez, Andrade, Horna, & Stern* 28807 (MO); *Krukoff* 8409 (MO).  
*Pseuduvaria* spp.: *NGF* 77112 (LAE); *Rogstad* 924.  
*Ruizodendron ovale* (Ruiz & Pavón) R. E. Fries: *Begazo* 61 (MO); *Klug* 3798 (MO).  
*Stelechocarpus cauliflorus* (Scheffer) R. E. Fries: *Rogstad* 998.  
*Unonopsis floribunda* Diels: *Gentry* 7452 (MO).  
*U. panamensis* R. E. Fries: *Johnston* 1643 (MO).  
*U. pittieri* Saff.: *Contreras* 10031 (MO); *Lent* 2289 (MO).  
*U. spectabilis* Diels: *Maas et al.* 6229 (MO).  
*Uvaria boniana* Finet & Gagnep.: *W. T. Tsang* 23823 (MO).  
*U. calamistrata* Hance: *Lau* 468 (MO).  
*U. confertiflora* Merr.: *Elmer* 21081 (A).  
*U. grandiflora* Roxb.: *Rogstad* 629.  
*U. javana* Dunal: *Elmer* 20857 (MO).  
*U. littoralis* Blume: *De Vogel* 3895 (MO).  
*U. lucida* Benthham: *Faden* 74/1251 (MO); *Pawek* 12051 (MO).  
*U. mendesii* J. Paisa: *Mendes* 639 (MO).  
*U. muricata* Pierre & Engler: *Gentry & Pilz* 32795 (MO).  
*U. osmantha* Diels: *Mendes* 673 (MO).  
*U. ovata* A. DC.: *Jacques-Georges* 5850 (MO).  
*U. poggei* Engler & Diels: *Robyns* 4227 (MO).  
*U. sabrida* Oliver: *Gossweiler* 10417 (MO).  
*U. sofa* Elliot: *Jacques-Georges* 14602 (MO).  
*Xylopiella elliptica* Maingay ex Hooker f. & Thomson: *Yeob* 5037 (SING).  
*X. ferruginea* (Hooker f. & Thomson) Hooker f. & Thomson: *Rogstad* 703.  
*Xylopiella* sp.: *Rogstad* 816.  
 Unidentified species: *Rogstad* 928, 961, 969.



**APPENDIX 2. Species of *Polyalthia* examined for leaf papillae\* and for thickened, straight anticlinal walls in adaxial epidermal peels.†**

- P. amygdalina* (A. Gray) Gillespie: *E. H. Bryan, Jr.* 509.  
*P. borneensis* Merr.: *Elmer* 21733.  
*P. cauliflora* Hooker f. & Thomson (sensu lato): *Kiah* 32101; *Mohd. Shah* 167; *S* 16620.  
*P. celebica* Miq.: *bb* 17290.  
*P. cinnamomea* Hooker f. & Thomson: *Henderson* 35168.  
*P. clemensorum* Ast: *Poilane* 29657.  
*P. consanguinea* Merr.: *Chun & Tso* 44029.  
*P. corticosa* Finet & Gagnep.: *Poilane* 19623.  
*P. debilis* Finet & Gagnep.: *Pierre* 289.  
*P. evecta* (Pierre) Finet & Gagnep.: *Poilane* 17313.  
*P. flagellaris* (Becc.) Airy-Shaw: *Chew Wee Lek* 1177.  
*P. jenkinsii* (Hooker f. & Thomson) Hooker f. & Thomson: *Chun & Tso* 43798.  
*P. lateriflora* (Blume) King: *Elmer* 21013.  
*P. littoralis* Boerl. (sensu lato): *Poilane* 19707.  
*P. longifolia* (Sonn.) Thwaites: *Wight* 35.  
*P. micrantha* Boerl.: *Buwalda* 7241.  
*P. microtus* Miq.: *SAN A* 3668.  
*P. modesta* Finet & Gagnep.: *Poilane* 17782.  
*P. motleyana* (Hooker f.) Airy-Shaw: *Chew Wee Lek* 1008.  
*P. nemoralis* DC.: *Pételot* 5955.  
*P. obliqua* Hooker f. & Thomson: *Hallier* 1774.  
*P. oligosperma* (Danguy) Diels:\*\* *Capuron* 20030.  
*P. oliveri* Engler: *Thomson* 109.  
*P. parviflora* Ridley: *Poilane* 704.  
*P. plagioneura* Diels: *Poilane* 29564.  
*P. rumphii* (Blume) Merr.: *FRI* 14190.  
*P. simiarum* (Hooker f. & Thomson) Hooker f. & Thomson: *Khant D.R.* 1174.  
*P. stenopetala* (Hooker f. & Thomson) Ridley: *Kiah* 36162.  
*P. suaveolens* Engler & Diels:\*\* *Kennedy* 1544.  
*P. subcordata* (Blume) Blume: *Korthers s.n.*  
*P. suberosa* (Roxb.) Thwaites: *Poilane* 5185.  
*P. tenuipes* Merr.: *Richards* 2306.  
*P. venosa* Merr.: *Ramos & Edaño* 36558.

\*See also APPENDIX 1.

†Papillae similar in structure and distribution to those of the *Polyalthia hypoleuca* complex were lacking in all species listed; the two species with similar thickened anticlinal walls are marked with double asterisks. All specimens are at A.

**APPENDIX 3. Characters used in the morphometric analyses of the *Polyalthia hypoleuca* complex.\***

I. Floral and vegetative characters.

A. Continuous (measured; in mm unless noted) and meristic (counted) characters used in multivariate data sets.

1. Androecium width.
2. Torus width.

\*For measurements of mature leaves, an average-size leaf on older growth was subjectively chosen.



3. Pedicel distal width.
  4. Stamen number.
  5. Carpel number.
  6. Inner-petal length.
  7. Outer-petal length.
  8. Androecium height.
  9. Pedicel basal width.
  10. Stamen length.
  11. Gynoecium width.
  12. Torus height.
  13. Inner-petal width.
  14. Outer-petal width.
  15. Stamen inner theca length.
  16. Carpel length.
  17. Pedicel length.
  18. Distance of gynoecium emergence above androecium.
  19. Flower number per leaf axil.
  20. Distance from distal peduncle articulation to base of pedicel bract.
  21. Stigma length.
  22. Outer theca length.
  23. Peduncle length.
  24. Stamen width.
  25. Lamina length (in cm).
  26. Lamina maximum width (in cm).
  27. Leaf drip-tip length (measured from inflection point of distal lamina border and border of drip-tip; in cm).
  28. Leaf primary vein number (counting only largest class of veins branching directly from mid-vein).
  29. Petiole length.
- B. Characters used in conjunction with results of multivariate analyses.
1. Number of latest flush of vegetative growth bearing flowers.
  2. Flowers in axils: of present leaves = 1; of abscised leaves = 2.
  3. Tree height (in m).
  4. Bole diameter at breast height (in cm).
  5. Inflorescence type: flowers with reduced peduncles (< 2 mm long), lateral buds and flowers lacking, large tubercles built up of old inflorescence scars lacking = 1; similar to 1, but tubercles present = 2; peduncles generally longer than 2 mm, lateral buds (and/or developing lateral flowers) and tubercles present = 3.
  6. Peduncle bract number.
  7. Lowest peduncle bract position with respect to stem bearing inflorescence: abaxial = 0; adaxial = 1; abaxial and adaxial on same specimen = 2; all angles (as on tubercle) = 3.
  8. Medial pedicel bract: present = 0; lacking = 1.
  9. Pedicel color: tan-brown = 1; dark red-black = 2.
  10. Peduncle and pedicel pubescence: lacking = 0; present only on peduncle = 1; tomentum = 2.
  11. Sepal pubescence (abaxial surface): lacking = 0; present on margins only = 1; present over entire surface = 2.
  12. Outer petal shape: no constriction, linear = 1; basal portion clawed, distal portion linear = 2; basal portion clawed, distal portion obovate or flared = 3; no constriction, ovate-obovate or elliptic = 4.
  13. Portion of inner petal where pubescence begins on adaxial surface: basal  $\frac{1}{3}$  = 1; middle  $\frac{1}{3}$  = 2; distal  $\frac{1}{3}$  = 3.



14. Color of adaxial, glabrous (basal) portion of inner petal: light tan-brown = 1; brownish red to wine red = 2; dark reddish black = 3; deep purple = 4.
15. Inner petal pubescence: sparse throughout = 1; moderate throughout = 2; dense throughout = 3; sparse throughout except dense on abaxial surface at base = 4.
16. Mid-vein of outer petal on abaxial surface: not detectable = 0; easily seen = 1.
17. Gynoecium emergence: all stigmas depressed below androecium = 0; stigmas level with androecium = 1; stigmas emergent above androecium = 2; stigmas and portion of carpels emergent above androecium = 3.
18. Stigmas: central ones depressed = 1; all level = 2; central ones raised = 3; all separate, radiating = 4.
19. Gynoecial area of torus: concave = 0; level = 1; convex = 2.
20. Apices of stamen connectives: concave = 0; flat = 1; mixed = 2.
21. Inner thecae of stamens: not touching = 0; touching = 1.
22. Color of carpel: all tan = 0; distal, abaxial surface deep red-brown, becoming tan basally = 1; all red-brown = 2; all dark reddish black = 3.
23. Carpel pubescence: lacking = 0; present on abaxial apex only = 1; present on abaxial apex with some on ridged sides and/or stigmatic crest = 2; present throughout = 3.
24. Shape of stigma: spherical = 0; elongate = 1.
25. Outer ring of carpels with very strongly curved carpels: no = 0; yes = 1.
26. Pubescence on youngest stems: lacking = 0; sparse = 1; moderate to heavy = 2.
27. Pubescence on petiole of smallest leaf: lacking = 0; sparse = 1; moderate to heavy = 2.

## II. Fruit and vegetative characters.

- A. Continuous (in mm unless noted) and meristic characters used in multivariate data sets.
  1. Pedicel length.
  2. Pedicel distal width.
  3. Mature carpel stalk length.
  4. Mature carpel stalk distal width.
  5. Mature carpel length, including only seed-bearing portion above stalk.
  6. Mature carpel width.
  7. Lamina length (in cm).
  8. Lamina maximum width (in cm).
  9. Leaf drip-tip length (measured from inflection point of distal lamina border and border of drip-tip; in cm).
  10. Leaf primary vein number (counting only largest class of veins branching directly from mid-vein).
- B. Characters used in conjunction with multivariate data analyses.
  1. Pedicel pubescence: lacking = 0; sparse or irregular = 1; dense tomentum = 2.
  2. Mature carpel apex: rounded or blunt = 0; acute = 1.
  3. Dried mature carpels with longitudinal ridges: no = 0; yes = 1.
  4. Stamen scars:  $< 40 = 0$ ;  $> 40 = 1$ .
  5. Tree height (in m).
  6. Bole diameter at breast height (in cm).